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SEXUAL PHOTOPERIODICITY

By THOMAS HUME BISSONNETTE

Trinity College, Hartford, Connecticut, and Marine Biological Laboratory, Woods Hole, Massachusetts

INTRODUCTION

IT IS now comparatively well known that seasonal sexual reproduction in some plants and animals is conditioned to greater or less degree by the relative lengths of day and night, by the intensity of illumination, and, in some cases, even by the color or wavelength of the light used to vary the length of day. This is not equally true of all plants nor of all animals. Other factors of the environment and hereditary or constitutional factors also influence the type and time of the manifestations of sexual activity.

It is proposed to discuss these phenomena briefly in attempting to see (1) how far one may go in classifying plants and animals on the basis of the relation of their sexual reproductive cycles to light in its various aspects, and (2) how the facts concerning these relations have been ascertained. Special emphasis will be laid upon the recent studies on animals; but the situation in plants, which is perhaps more completely known, will be reviewed briefly first.

SEXUAL PHOTOPERIODISM IN PLANTS

As early as 1890, Curtele (7) found that light intensity was a factor related to blooming and fruiting in some plant species, that some failed to bloom in very diffuse light and that the number of blossoms and the size of fruits were smaller in diffuse than in bright light. Vöchting (43) confirmed these findings and showed that under weak illumination the formation of flowers in numerous plants was either prevented or rendered imperfect and that blooming was correlated with the activities of leaves. Schimper (40) pointed out that "shade plants" bloom on a lower minimum intensity of light than do "sun plants," yet "shade plants" produce fewer flowers.

Even forty years ago, therefore, it had begun to be suspected (1) that there was some relation between length of day or type of illumination and sexual activity; (2) that sexual cycles or activities were not entirely matters of internal rhythm fixed by hereditary constitution and entirely independent of environment; (3) that temperature cycles might not be the

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major factors conditioning seasonal reproductive cycles.

Klebs (24) was one of the first to investigate this problem experimentally in an attempt to modify the blooming time of *Sempervivum*, a plant which normally blooms in June. By increasing its daily period of illumination he induced it to bloom in winter.

But it remained for Garner and Allard (13, 14, 15, 16, 17, 18, 19), Adams (1, 2, 3), and others (4, 12, 21, 28, 9, 42, 23, 29, 31) to make a broad systematic study experimentally of the relation of onset of blooming, including sexual reproduction, in many plants to the relative lengths of day and night and to changes in this relationship. Garner and Allard (13) laid the foundation for and formulated a classification of flowering plants on this basis. They coined the word "photoperiodism" for the response of plants to changes in relative lengths of day and night by beginning to bloom, or to their exhibition of "sexual" photoperiodicity. They reached the conclusion, which subsequent research has continued to support, that flowering plants fall into three classes so far as photoperiodism is concerned;—(1) Short-day plants, which begin to bloom when days are shorter than 12 hours long or when, naturally or artificially, they become shorter than a critical or usual length; (2) Long-day plants, which come into bloom when days lengthen or become longer than a critical length in relation to nights; (3) Ever-blooming or indifferent plants, which complete their reproduction without definite relation to the day-night ratio or within very broad limits of day-length (23, 31).

Wann (44) tested the photoperiodism of *Marchantia polymorpha*, a bryophytic non-flowering plant, and found that its gametophyte is a long-day plant in its sexual reproduction.

Garner and Allard (13, 15) and Kellerman (23) show that this response is quite definitely localized. Even the top and bottom thirds of a plant, like late-blooming *Cosmos*, can be brought into blooming by experimental alterations of their periods of exposure to light while the middle third is kept growing vegetatively without flowering, and *vice versa*. They found that very weak light from electric bulbs, as low as one one-thousandth of the intensity of sunlight and almost lacking ultra-violet and some other constituent wave-lengths of sunlight, was enough to bring on flowering in some long-day plants. Wave-length did not seem to matter much in this response, though it does for growth (32) and germination (11). Flammarion, about 1898 (10) (cited from Garner and Allard (13)), however, had found that some plants bloomed earlier in red light than in white. The lower limits of effective intensity do not seem to have been determined yet. Garner and Allard (23) found that alternate single hours of light and darkness were not equivalent to twelve hours of light followed by twelve of darkness. But a period of two hours of darkness in the middle of the twelve hour period of light did not appreciably lessen the response, though the light time per day was thereby reduced to ten hours. So it takes some time for the response to get under way, and the momentum of the reaction bridges a two-hour gap of darkness.

The fundamental chemical internal changes in the plants upon which the inception of reproductive activity directly depends have not yet been determined beyond controversy. Some have suggested changes in sugar concentration (24), in H-ion concentration of the sap (20) or in carbohydrate-nitrogen ratio (22, 27).

The relations of sexual photoperiodism to other environmental factors,—tempera-

ture, humidity, and available carbon-dioxide,—have been studied. It has been shown that response to changes of period of light can be modified by changes in these other factors in some cases (8, 22, 5, 6, 29, 41). If the light period is suitable for a particular plant, it will bloom as quickly as climatic conditions permit; but if the light period is not suitable, weather changes cannot cause flowering (23).

Since 1919, Schaffner (34, 35, 36, 37, 38, 39), Richey and Sprague (33) and others have been finding that relative length of day and intensity of light influence the expression of maleness or femaleness in some plants such as hemp, maize, Jack-in-the-pulpit and others, and that this expression may be modified or even reversed experimentally by altering the length and intensity of daily illumination for these plants. Loehwing (25) has shown that male plants of long-day spinach and of short-day hemp have higher percentages of iron, magnesium and sugar, more soluble sap constituents, and greater oxidase activity of tissue fluids than female plants. This is in agreement with Manoilov's reactions (26) and with those of others.

SEXUAL PHOTOPERIODICITY IN ANIMALS

Studies on sexual photoperiodicity in animals will be treated more or less chronologically, though the early studies were independent of each other.

In 1698, Martin (103) reported "The inhabitants observed that when the April moon goes far in May the fowls (referring to sea birds) are ten to twelve days later in laying their eggs, than ordinarily they use to be." This suggested an influence of moonlight as well as sunlight on the reproductive periodicity of wild fowl.

In 1907, on theoretical grounds, Sharpey-Schafer (120) suggested that the regularity with which migration occurs (in birds) indicates that the exciting cause must be regular. There is no yearly change outside the equatorial zone that occurs so regularly in point of time as the change in the duration of daylight. On this ground this may well be considered a determining factor in migration, and it has the advantage over other suggested factors that it applies to the northerly as well as to the southerly movement.

He said further, however, "that it is the result of developmental changes in the sexual organs is improbable." This was because the sex-glands of spring migrants were still about as small as in autumn.

Keeble (94) described the peculiar cyclic behavior and breeding activities of two worms of the genus *Concoluta*. Egg-laying reaches its maximum when the animals are exposed to only six hours of light each day, at intervals of two weeks, in relation to spring tides or under experimental conditions. They, therefore, correspond to short-day plants. There are many other cases of such periodic behavior among aquatic invertebrate animals; but it is open to question whether they are true cases of sexual photoperiodicity. So they are not included here.

Marcovitch (98) studied plant lice or aphids in which sexual individuals usually appear in autumn. It was believed that falling temperature was the cause of their appearance. He showed, however, that the much more marked and regular shortening of the days was the major environmental factor concerned. The strawberry root louse (*Aphis forbesi*) normally produces sexual individuals in November and the eggs hatch in February. By subjecting very young individuals to days of about eight hours soon after hatching, he induced the appearance of sexual individuals on May 7 and egg-laying on May 22. Temperature was not a factor. Migration of the aphids in autumn, which precedes the appearance of sexual individuals, was also conditioned by relative

length of day in several species. Males and sexual females were obtained in June in high temperatures by keeping them and their host plants exposed to short days for about seven weeks. He also found that the rosy apple aphid (*Aphis sorbi*), in which migrants may occur in any generation after the third in spring, responds to increasing length of day by producing migrant individuals. They would, therefore, correspond to long-day plants, while the others mentioned above would correspond to short-day ones.

Eifrig (81), on purely theoretical grounds, suggested that bird migration is a response to change in length of day but is not dependent on sex-gland changes.

Experimental studies on birds

Before 1925, Professor Rowan (110, 111, 112, 113, 114, 115, 116) of the University of Alberta, Edmonton, began his studies on the relation of changes in length of day to migration of the snow bird (*Junco hiemalis*). In Edmonton, the temperature in winter falls below −50°F. By a series of experiments carried out in open cages in winter, he showed that reversing the daylight curve in autumn and winter, by adding electric light after nightfall in increasing periods, would cause the sex-glands of juncos, canaries, and crows to enlarge and produce sperms in winter instead of at the normal breeding season in April or May. In juncos and crows, this enlargement was correlated with the tendency to migrate north. Southward migration was correlated with regression or diminution of sex-gland size and activity, which could be brought about by shortening their daily exposure to light. Weak light from electric bulbs was sufficient to bring about the breeding condition four or more times a year if added after nightfall for a time and then withheld. His interest was primarily with the relation of migration to cyclic seasonal changes in length of day. He concluded that migration is dependent on cyclic changes in the sex-glands, and called this group of responses "photoperiodism" after Garner and Allard (13). Rowan has suggested, and his evidence, though incomplete, in general supports the idea, that juncos and crows migrate northward toward longer days when their sex-organs are increasing in activity, and southward toward longer days when the organs are regressing or have regressed to a certain stage in autumn as the result of shortening days in the northern regions.

We are not interested primarily in the migration problem, but in the reaction of the sex-glands to changes in length of day. Nevertheless, on the basis of our studies on starlings and ferrets and of some of Rowan's own data on castrate crows and migration, it may not be too foolhardy to suggest that possibly the migration urge originates beyond the sex-glands and depends on states of the activities of the anterior hypophysis. Evidence is accumulating to show that the hypophysis is responsive to light stimuli based on length of day in some animals (89, 90, 91, 92, 59, 63, 64, 67, 68). It is known to control the activities of the sex-glands and, through them, the accessory sexual apparatus and behavior (76, 77, 78, 87, 88, 121, 122, 117, 118). It is, perhaps, not going too far to credit it with the migration urge also as an early phase of the drive toward mating reactions in spring, and as a phase of the reaction from it in autumn. The bases for this suggestion may be more evident after later studies have been described.

Unfortunately Rowan (113) on the basis of a very limited and, therefore, misleading experiment, using increased exercise with reduced lighting periods on some birds already well advanced in sex-

gland activation in March, came to the conclusion, and still maintains, that "It would thus appear that radiation may be definitely eliminated and that increasing exercise suggests itself as being responsible for the recrudescence of the organs of the junco. The extra consumption of food for reasons discussed elsewhere is of questionable significance." As will appear later, in starlings and some other forms at least, it *is* the increase in periods of light, as such, that modifies the sexual cycle, and *not* the increasing exercise. The results of work by Bissonnette and others cited above support his statement about the relative unimportance of amount of food consumed, above the minimum to prevent inanition. But it is quite evident that quality or variety of food does act as a limiting factor, and plays an even more important rôle in some cases. Longer feeding periods or shorter night periods without feeding have been looked upon by poultrymen as the cause of the increased laying of fowls in autumn and winter when they are subjected to "night lighting." But experimental studies on birds by Rowan, Cole (73), Miyazaki (105, 106), Benoit (53), myself (54–73 inclusive) and others (86) and similar studies on sexual photoperiodicity in mammals (47, 48, 50, 51, 52, 61, 63, 65, 67, 69) and Amphibia (119, 127) rather indicate that the larger consumption of food is the result of increased reproductive or sexual activity, instead of its cause.

Between 1926 and 1928 Bissonnette and Chapnick (70) and Bissonnette (54, 55) and since that time, Bissonnette and Zujko (74) studied the normal sexual cycle of the European starling (*Sturnus vulgaris*), a bird which migrates only very little in this country. At Hartford, Connecticut, they form great flocks in autumn and winter and roost around buildings and sometimes in trees in the city at night and spend the day scouring the country for insects and other food. Birds were killed for study of their sex-glands at approximately fortnightly intervals. The changes were checked for a second year and an attempt was made to find some correlation between the observed changes in the sex-organs and some regularly changing factor in the environment such as temperature, barometric pressure, daily hours of daylight, etc. It was impossible to ascertain types of food or its amount at the various times or the daily intensity of illumination, since the birds were taken from nature and had free range.

Of all the environmental variables tested over the period of study, daily hours of daylight increased and decreased uniformly from year to year in close correlation with the changes of the sex-glands occurring at the same dates each year. Temperature and barometric pressure varied very irregularly and increase in testis size and activity appeared to bear no consistent relation to them (70).

An experimental study was therefore begun to ascertain whether or not there is any close correlation of the ebb and flow of the tides of sex-gland activity with the waxing and waning of daily periods of light. Rowan's theory (113) that cycles of daily hours of exercise rather than hours of light were the fundamental cause of sexual cycles did not seem to be demonstrated beyond question by his very limited experiment nor to be the only explanation compatible with his data. So it was tested along with the effectiveness of increased lighting without forced exercise, against controls without added light or exercise.

Apparatus modelled after Rowan's, but with improvements to increase its effectiveness, was used to disturb the birds in one cage from their roost and the floor every 20 seconds for definite periods after

nightfall increasing up to seven hours per night. Birds in another cage were subjected for equal periods each night to light from 60-watt bulbs. Those in another cage were not lighted or exercised after nightfall. Experiments were carried out from December to April inclusive.

Added exercise periods without added light, were not only ineffective to induce activity of the sex-glands, but tended to reduce both the sizes of the testes and their germ-cell activity. Added light, on the contrary, proved to be a very potent stimulant for activation of the sex-glands of the starling (56).

By modifying the experimental method and the previous sexual condition of the birds used it was found that increasing exercise periods led to a lag in onset of changes in the testes induced by changes in day-length, whether these changes consisted of increase of activity induced by increasing exposures to light or of decreasing activity or regression consequent from reduced lighting. Increased periods of exercise merely fixed the trend of change in testes operating before changes of lighting, of exercise, or of both occurred. The delay in activation due to this lag or prolonged refractory period was usually more than made up for later by increased acceleration of changes of the testes, once the changes had begun (56).

Exposures to light after sundown, up to six or seven hours per night, led to complete spermatogenesis and maximum size of the testes (sometimes greater than the natural spring maximum) in from four to six weeks at any time between November and May. Controls subject only to short daily periods of light, like those of winter, did not come into activity even in April, May or June, when, in nature, the testes are at maximum size and activity, or past it. The testes of birds on forced exercise periods added to short winter-like daily periods of light became smaller and less active in spermatogenesis than those of controls without added periods of light or exercise. The state of activity of the testes (and of ovaries as judged by gross inspection at autopsy) could be modified at will in either direction, within the limits of their natural changes, by increasing or decreasing their daily periods of illumination. Some birds could also be kept a month or more in a condition of partial regression by holding constant their daily periods of light and exercise, once the increase or decrease of activity had been stopped by the constant light period (56).

Further studies (57, 58, 71, 72, 73) aided by grants from the National Research Council, Committee for Research in Problems of Sex, showed that the rate or degree of stimulation of testis activity varies with the intensity of illumination used, since birds under a 10-watt bulb were slower to reach maximum activity than those under a 15-watt bulb, and these again than those under a 25-watt bulb, and so on. Birds with added periods of both light and exercise were slower to begin activity, but later overtook those with added light of similar intensity alone. The optimum intensity or duration of the daily period have not yet been determined.

The degree of stimulation for starlings depended also on the color or wave-length of visible light used (58, 71). Red was found to be very highly stimulating. Green of equal luminous intensity, used for the same daily periods, was not stimulating, but was rather inhibitory to activities of testes and ovaries in the great majority of cases. White light was less effective than red of the same luminous intensity, probably because of smaller content of red or other stimulating rays. With much lower luminous intensity,

violet light was apparently slightly inhibitory. This difference in the effect of red, green, white and violet lights was not due to heat or total energy intensity but to apparent wave-length specificity.

That this apparent specificity of wave-length in the visible spectrum for sex-gland stimulation is not found in all animals has been shown by Marshall and Bowden (102). They found all wave-lengths tested, between near infra-red and near ultra-violet, to be effective in activating the sex-organs of ferrets. Within these limits, intensity and duration of light were the most important factors. Beyond these limits of wave-length, radiations were not effective.

In starlings, daily period, intensity, and wave-length of light reaching the birds are factors in controlling the seasonal sexual cycle when diet is adequate, varied, and rich in vitamins, proteins, salts and fats. On a "middlings mash" diet, however, without added vitamins, proteins, salts or fats, even red light of higher intensity than that used in the preceding experiments was almost completely prevented from inducing any increase in sexual activity in starlings in January (64). So improper food, even in sufficient quantity, acts as a limiting factor which may prevent even highly stimulating exposures to light from inducing sexual activity, or greatly reduce its effectiveness.

No mating or egg-laying in starlings was observed under these experimental conditions, even in birds brought to complete sexual maturity, as judged by histological criteria. Mating and laying in these wild birds seem to be controlled by factors outside the crowded conditions in these experiments and not by mere gametogenic fitness for breeding, as judged histologically only (63, 64). Professor L. J. Cole (75), however, by similar methods, induced mourning doves, which do not breed naturally in autumn and winter, to mate and produce viable eggs in winter. These doves will breed in captivity in their proper season without the added light stimulation.

With starlings a maximum effect and consistent results were obtained by giving large and immediate increases in daily periods of light with electric light, rather than by gradually increasing periods, even in autumn when daily periods of daylight decrease. Filtered red light of 1.7 foot candles luminous intensity, acting for six hours each night from the start, after nine and a half hours of daylight gradually decreasing with the season in a basement room, induced complete spermatogenesis in 23 days in December and January. Other combinations including red light did it in 18 days (56, 57, 58, 71, 72, 73).

Normally testis regression in starlings apparently occurs invariably before June 8 or 15, for no birds killed on those dates or later had remained at complete spermatogenesis (55). But the daily periods of light are still increasing slowly up to June 21, in both duration and intensity. Experimental studies indicated that, even with the most potent schedules of lighting used, birds invariably passed the climax of testis activity and size after a time and underwent regression. This regression was more or less independent of the proportions of ultra-violet or green in the light used. It was due to a "throwing out of gear" of some part of the sexual or reproductive mechanism. Even with the most stimulating exposures to light used, it was impossible to maintain maximum testis size and activity beyond a certain period which varied with the times occupied by the activation phases of the cycle. The time occupied by any phase of the sexual cycle appeared to bear an inverse relation to the effectiveness of the light stimulus used. Animals quickly brought

into maximum activity remained in complete activity for a shorter time than those more slowly activated (57, 58, 71, 72). This loss of activity, even on high stimulation, occurs in male and female ferrets also (65, 67, 68). Long continued injections of gonadotropic hormones from the anterior pituitary and from "pregnancy urine" have shown this same sort of failure to maintain activity of the sex-glands and secondary sexual characteristics in rats, rabbits and even in monkeys according to Collip and his associates and to Meyer and Gustus (49, 76, 77, 78, 117, 118, 104).

A grant from the Grants-in-Aid Committee of the National Research Council and a sabbatical leave from Trinity enabled me to study at Cambridge University in 1931–2 to extend these studies on the starlings and to begin similar studies on ferrets. These mammals have a seasonal sexual cycle or periodicity like that of the starling.

An unsuccessful attempt was made to determine whether the light affected the starlings through the head. Light-tight hoods were used upon half the birds in a cage while added exposures to light were made. But all the birds in the cage died as the result of the handling of the birds to put on and take off the hoods, and nothing came of it. However, the experiment on defective diet, described above, was carried through and its results were taken to show that, if either the light exposures or the diet be too restricted, sex-gland activation fails to occur. This may throw some light upon the sexual cycles and reactions of tropical birds as these may be related to changes of food and of light. This has been discussed in previous papers (61, 63, 64).

Last December, Benoit (53) showed that ducks respond to increased length of day by increased sex-gland activity during their quiescent period. He found that the eyes were the receptors of the light stimulus. Ducks with their eyes covered but the rest of the body exposed were not affected by increased length of day; while those with bodies covered and eyes exposed were. We have had similar experience with hooded ferrets (67, 68, 69, and unpublished data).

Miyazaki (105, 106) has shown that a green bird of Japan called the mejiro (*Zosterops palpebrosa japonica*) can be brought into sexual activity at least three times each year, instead of once as in nature, by the practise of "yogai." This consists of adding illumination at night. It has been practiced for many generations in Japan to induce early mating-song in these birds. Reduction of daily light period led to moulting.

In a private communication, Dr. Scott of Kansas State College of Agriculture tells me that he has induced mating and laying with turkeys in January instead of March by night-lighting but was unable to get any effect if the lighting was merely given during the daytime as additional intensity. Neither was he able to obtain any effects upon Guinea fowl with night lights. This is an interesting difference between the turkey and the Guinea fowl. The former is native to the temperate zone and has been subject to natural selection for seasonal breeding in spring, probably on the basis of reaction to light cycles, for countless generations, in which those not properly related to the season were eliminated by adverse climatic conditions at a critical period in their early lives. The Guinea fowl was native to the tropics where such selection would be absent, much less rigorous, or based upon some other environmental factor.

For many years domestic fowl have been induced to increase egg-production in autumn and winter by "night-lighting"

(125). The first account of such use of night-lights with poultry is traceable to a Spanish book of 1802. But Waldorf was the first to use this method in this country in 1895, according to Lippincott and Card (95). By 1920 almost all commercial poultrymen in some states were using it. It is known now that fowl may be bred to high autumn and winter production without the aid of night lighting. In hens the response to it is evident in ten to twelve days.

Dr. Callenbach of Pennsylvania State College tells me in a private communication that he has found that the temperature of the brooder in which chicks are raised can make a difference in the time at which pullets reach sexual maturity and lay their first eggs, when lighting conditions are constant.

As the studies on starlings stand, both light and diet appear to be factors in the control of sexual cycles,—light more than diet. Other factors not yet tested may also modify the response.

Experimental studies on mammals

The normal seasonal sexual cycles of male (45, 46) and female ferrets (83, 99) have been very thoroughly studied. The animals come into sexual activity once a year and have a long period of sexual quiescence. Males complete spermatogenesis between February 12 and 20 and become aspermic or unable to breed in late August. Females come into oestrus or breeding condition in March or early April and remain in heat when unmated till late August. Ovulation occurs only after the orgasm of copulation and between 34 and 36 hours after the beginning of copulation according to my experience, 30–40 hours according to others using larger numbers (99, 83, 84, 85, 87, 88). Pregnancy and pseudo-pregnancy are of equal length, about 42 days, and females usually come into oestrus a second time if either suckling or pseudo-pregnancy terminates before the end of August. The animals are easily kept in the laboratory and often become quite tame and tractable. One great advantage offered by ferrets for studies of this kind is that, when oestrus approaches, the vulva or margin of the opening of the female reproductive passages begins to swell and finally reaches the diameter of about three-quarters of an inch or less when the receptive stage of oestrus comes on. This obviates the necessity of taking smears of the vagina walls and makes it plain when oestrus occurs. The swelling subsides at the beginning of anoestrus and disappears entirely during the long winter season from August onward, or when pregnancy or pseudo-pregnancy follows copulation.

In my work with these animals only small numbers have been used in any one experiment. But variations in experiments and their results have served as checks on each other and the results have been consistent throughout and with those of others for the most part, though my conclusions and theirs have not always agreed in detail.

Before the experiments to be described below (59), it was held by various students that the sexual cycle of the ferret was not amenable to control by changes in time of illumination or the light to which it was exposed (88, 126). A ferret had not been known to come into oestrus or breed in the northern hemisphere between September and February inclusive, except as the result of injections of gonadotropic hormones from the anterior hypophysis or pregnancy urine. Males did not even become fertile under these treatments (88). Nor did either sex after treatments with small doses of ultraviolet (88).

On October 12, three females and three males were placed in six rabbit cages in two vertical rows, females in one and males in the other, facing a large double window left partly open at all times. A 200-watt electric light bulb was fastened in a clamp at such height and distance from the cages that it threw light directly into all six, from just above the floor-level of the upper cages and to the back of the floor of the lowest. This triangulation kept the distance constant and the animals always in direct light when light was on. Luminous intensity in the cages under experimental light varied from about 4.9 foot candles at the back of the lowest cages to about 14.1 at the front of the upper ones. Light was turned on for six hours each night after nightfall by a time switch, in accordance with the finding for starlings that immediate maximum increase of exposure to light would give best results. These experimental animals were not given nest boxes to sleep in, but only scanty shavings to make shallow beds and to keep the cages dry. This prevented them from keeping as warm as controls, kept in a similar room across the hall with nest boxes and somewhat more general daylight because of larger window area. Windows in both rooms were kept open at all times and temperatures varied with that outside with the season. Drafts from the windows swept across the space between the lamp and the cages. Food was uniform for all animals.

Ferrets spend most of their time curled up in sleep with their heads in the middle of the circle formed by the body, except when sexually active, when they run back and forward across the fronts of the cages more than during anoestrus. This position of the head had a slight effect on rate of activation in different cages under the conditions of these experiments because the heads were somewhat shielded from direct horizontal light but not from oblique or vertical light (59).

Before November 23 (42 days) two of the females were in complete oestrus; the third lagged till she was prevented from hiding her head in shavings on December 1. She came into oestrus on December 20. Controls showed no signs of oestrus till the regular time in March.

Two of the experimental males died from abscess in the head and from cause unknown on November 18 and 25 after 37 and 44 days of added lighting respectively. In spite of these fatal illnesses, their testes were enlarged and had increased in activity. The epididymis of one was modified toward the breeding condition. They were compared with those of a male purchased from a dealer and killed on December 12, as control. The testes of the surviving male increased in size, descended into the bottom of the scrotum and his scrotal hair became scanty. His libido became that of the breeding animal and his epididymis also. He mated successfully with the oestrous females on December 11, 12, and 21, for the characteristic long periods (10 minutes to 3 hours for ferrets) and the females were all pseudo-pregnant and underwent the changes incidental to that condition. The male was killed for study on December 22, the day following his last copulation, which lasted one hour and forty minutes. No sperms were found in the vagina of any of the females. His testes showed completely active interstitial cells correlated with an epididymis in full breeding condition; but the germ-cells in the tubules had not multiplied beyond the secondary spermatocyte stages, though they showed some evidence of an initial stimulation, followed by slow regression before he was killed. Control males had no sexual

interest in these females though the females were in complete oestrus. A male transferred from control to experimental light in November showed strong mating reactions even on December 12, though his testes were only slightly enlarged and he was not producing sperms (59).

Various modifications of the initial experiment were carried out, such as keeping the days constant in length with curtains, shortening the periods of daily light or reducing its intensity and so forth. Hoods have been used which covered the eyes and head, others which covered the head but not the eyes. Hypophyses have been removed from some ferrets and optic nerves severed in others. Added light periods have been tried on all such animals, with controls, and animals have been subjected to increasing periods of light for long periods and carried over for more than a year and a half to follow the late and after effects of the exposures to light (69).

Even in the early experiments the method used was fully effective on females. Ovulations followed copulations with light stimulated males that were still aspermic. It was thought that males were less susceptible than females to changes in length of day. This has turned out to be an incorrect conclusion in the light of experiments in which gradual increases in the length of day were made. Males are apparently more sensitive to changes in length of day than females and react more quickly to lessening day-length (67, 69). This accounts for the results in the first experiment in which the slowly decreasing daylight periods after the initial artificial increase in total time of light caused regression after an initial activation. This method brought females into complete oestrus and permitted them to continue in heat for some time (69).

Females kept at a constant daily daylight period in spring by the use of curtains came into a delayed oestrus on a constant seven and a half hour light period, as the result of increasing intensity of the daylight in April and May and of some light filtering around the edges of the curtain into the cages during that part of the day when the cages were curtained. But they went out of oestrus when moved into cages into which this additional light did not penetrate. Females brought into oestrus and kept in that condition for some time by light periods increasing up to 18 hours per day went into anoestrus when the periods of light were reduced to 16 hours as well as when reduced to 8 hours. So it was concluded that the previous light history of an animal or the light to which it had become accommodated or temporarily adapted, and its endocrine or physiological condition determines the effect of any given length of day. Increasing day-length induced oestrus in animals not already in oestrus; decreasing it induced anoestrus in those in oestrus or delayed oestrus in those already activated to begin activity of the sex-glands. But a good start into activation carried females into oestrus even when light-periods were slowly reduced after the initial impulse (69).

After comparing these results with results following treatment with gonadotropic hormones from the anterior hypophysis, we have suggested that the anterior hypophysis is stimulated by the increase in length of day and in its turn stimulates the sex-glands which control the accessory sex-organs and behavior (59, 67). This is in some respects like the effect of light and dark surroundings on various fish, reptiles, and crustaceans studied by Professor G. H. Parker and

others, in which humoral agents mediate the changes (108, 109).

Hill and Parkes (91, 92) have confirmed our results in the induction of oestrus in the anoestrous period in ferrets. They have shown that hypophysectomy obliterates sexual cycles and prevents increased lighting from inducing oestrus in ferrets, and we have confirmed this. They have shown that both male and female ferrets come into sexual activity and breed, if, after normally increasing days to January 24, they are confined in total darkness for 23½ hours or more per day, though the coming of oestrus is delayed in females, at least. One female bred twice in the five and a half months of the extremely short periods of light. Possibly the initial stimulus of 34 lengthening days was enough to carry the animals into complete sexual activity, though more slowly after the reduction of periods of light (102). The males were already within 12 to 14 days of the coming of sperms on the normal cycle (46). If this is the case these results are consistent with ours and with those of Marshall and Bowden (102).

Our first experiments with males did not induce complete sperm production in autumn or winter. But by increasing the daily period of light gradually up to seven or eight hours per night from October 2 onward with males over one year old, instead of with those not yet fully grown, we have succeeded. Sperms have been produced as early as November 7 [the low point in the normal cycle (45)] and copious ejaculations of sperms in matings on November 26 (65). Allanson, Rowlands and Parkes (47) obtained fertile matings on December 29, from a male, by increased length of day followed by injection of urine of pregnancy extract. Some of their males came into spermatogenesis in January on increased lighting periods alone. But pregnancy urine usually stimulates only the interstitial cells, and not the germ-cells which are stimulated by the hormones of urine from castrates and from persons past the menopause (121, 122). So it is doubtful if their injections hastened the spermatogenesis.

We have good evidence that there are two factors affecting the testis, differentially stimulated as to their production by the increase in length of day. The factor most quickly stimulated in ferrets by light acts on the interstitials and these activate the accessory organs and libido. This factor also continues to act longer than the second one. This second one acts upon the germ-cells and induces spermatogenesis. It is more susceptible to reduction of day and, in the ferret, is the first to cease to be effective when regression of the testis begins, independently of the increasing length of day. Both factors, however, fail to remain effective beyond a certain period and regression sets in, in spite of lengthening days, just as in the starling (59, 65, 67, 68, 69). Similar changes occur in long-continued administration of gonadotropic hormones from the anterior hypophysis and urine of pregnancy (49, 76, 77, 78, 117, 118, 104) with rats, rabbits and monkeys. The hypophyses of these male ferrets were modified histologically and cytologically by the changes in length of day in correlation with the changes in the sex-glands (65, 67).

Baker and Ranson (50, 51, 52), who started work on mammals before I did, have shown that, for field mice, length of day, type of food, and latitude are all factors in controlling sexual cycles. Allanson and Deanesly (48) have shown that hedgehogs respond to length of day, temperature and hormone injections.

These two species are therefore less stable than ferrets in their sex mechanisms and sensitive to more factors in the environment. Even the clawed toad of South Africa (*Xenopus laevis*) is affected by reduction of daily duration and intensity of light and its sex-glands undergo involution in captivity with reduced light (127, 119).

On the contrary, the Guinea pig shows practically no response to changes in length of day by changes in its sexual cycles. The time of night at which most females first show receptivity toward males is slightly shifted; but cycles are otherwise unaffected (80). The 13-lined ground squirrel (*Citellus tridecemlineatus*) shows no modification of its sexual cycle induced by changes in relation to light, according to Moore and his associates (107, 123, 124) and Johnson and Wade (93). Among fish, the stickleback responds to changes in temperature but not to those of light (79). Doubtless many other animals fall in these classes.

Most sheep come into oestrus and breed in autumn on a falling length of day and so come to drop their lambs in spring. Some breeds, however, appear to have two cycles of breeding times each year and are sexually active in both spring and fall (100). This is true also of other species, which, therefore, correspond somewhat to short-day plants. Ferrets, starlings, juncos, turkeys, etc. and those of their type correspond to long-day plants, though there does not seem to be a critical day-length for them as for plants. Their previous sexual and light histories evidently determine for the time the critical length of day. Relative direction of change of day-length seems to be the determining factor. Guinea pigs, Guinea fowl, ground squirrels and sticklebacks correspond to everblooming plants.

Even the women of Patagonia and the Eskimo fail to have sexual or menstrual cycles in the long arctic night and the men lose all sexual activity and libido also, to recover and resume sexual cycles when the daylight reappears in spring. Dr. F. Cook, who reported this from observations with the Peary Expedition in 1894, pointed out that the men of the Peary Party were affected similarly by the conditions (96).

CONCLUSION

It is already evident that there are numerous variations as among the different species in each class in relation to periodicity of sexual cycles associated with changes in length of day. In addition, many other factors, such as changes of temperature, food, humidity, and rainfall, play varying rôles (61, 101).

If we ask what has led to the differentiation of some species to respond to lengthening days, of others to shortening days, and of still others to be indifferent to length of day or to respond to other factors in the environment, or, perhaps, to none, we are compelled to fall back upon speculation or conjecture.

One may suggest that, in the countless generations of animals and plants living under different types of season, with different times of stress and danger to the offspring, *that* type of sexual cycle which best meets these obstacles to success and survival for each species has been evolved for it under natural selection. Those not producing their young in a favorable season died out, because their sexual cycles were not adapted to their environment. Those that most nearly conformed survived. Some species developed a relation to one factor in the environment which set off or controlled the sexual mechanism

at the right time, such as the very regular change in length of day. Sometimes they became related to it in one way like starlings and ferrets; sometimes in another, like sheep. This depended also on length of gestation period in some cases. Other animals and plants were better served by a factor like change in food (82), in temperature (79) or in humidity (61, 101), and were selected in relation to it.

We are still only in the beginnings of these studies of sexual photoperiodicity or photoperiodism and most of our conjectures must serve only as working hypotheses, to be tested out on each species in turn, in the hope that some great or broad correlating principle may emerge as the smoke of controversy and conflicting opinions clears with the increase of more definite knowledge. We must not deceive ourselves by thinking we have the keys to the whole of the problems as yet. They are still beyond our grasp, but coming nearer.

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THE SPINAL ACCESSORY NERVE AND ITS MUSCULATURE

By WILLIAM L. STRAUS, Jr. and A. BRAZIER HOWELL
Department of Anatomy, Johns Hopkins University

INTRODUCTION

THE fact that in mammals the so-called accessory field of musculature, comprising the trapezius and sternocleidomastoid muscles, is innervated both by ramus lateralis n. accessorii and by branches of the anterior rami of the cervical nerves, is a circumstance that has never ceased to puzzle anatomists. The present writers have been interested in this problem for a number of years and have borne it constantly in mind during the course of their investigations. At present it is almost universally believed that ramus lateralis n. accessorii is of visceral derivation. Recently, however, Addens (1933) has revived the old claim (see discussions by Fürbringer, 1897, and Lubosch, 1899) that this nerve is a spinal component of somatic origin.

Addens bases his contention on three main points: (a) the presence in a few fish of a component of n. X which he interpreted as somatic and the homologue of spinal n. XI; (b) the apparent continuity of the spinal XI nucleus with that of n. XII in some forms; and (c) the assumption of some investigators that m. trapezius is of myomeric rather than branchiomeric origin. Addens thus believes that the spinal accessory nerve and trapezius sheet of musculature have somatic rather than branchiomeric genesis, a contention requiring the thesis that in this respect mammals are more primitive than the dogfish.

If ramus lateralis n. accessorii be merely a modified somatic spinal component, then the dual innervation of the spinal accessory field of musculature involves no particular problem. On the other hand, if this nerve be of visceral derivation, the double innervation of its musculature is myologically unique. In such case either the muscles are of compound visceral-somatic origin, or else, primarily visceral, some of their nerve components have secondarily shifted to follow a somatic (spinal) pathway.

FUNCTION OF THE ACCESSORY FIELD OF MUSCULATURE

The functions of the sternocleidomastoid and trapezius muscles are well known, yet it appears advisable to stress certain features in the present connection. The former division not only nods the head and rotates it, but is of use in respiration for advancing the sternum. The trapezius is, perhaps, the most frequently used muscle of the shoulder. Its anterior portion advances and adducts the scapula voluntarily, fixes the shoulder for other movements, advances it in forced respiration, particularly in quadrupeds, and, above all, constantly maintains its posture. The middle part of the trapezius adducts the scapula, usually in synergy with the rhomboid, and the lower part retards it. It thus is seen how complicated is the rôle played by these muscles. Not the least important function is that concerned with respiration, this being most marked in forms which maintain contact of the fore feet with the ground. For example,

Longet (1861) found that if quadrupeds are made to run, following bilateral section of n. XI, they rapidly become breathless because of inability to advance the thorax.

MOTOR NUCLEI

Before considering peripheral conditions of n. XI, it is advisable to offer a brief résumé of the essential facts regarding the motor nuclei of the striated visceral musculature, as condensed from the literature (esp. Addens, 1933; Black, 1917, 1920; Kappers, 1920).

It is logical to assume that in the earliest phylogenetic stages, in which continuity of the branchial elements was relatively complete, there was a single, continuous column of branchial motor nuclei, including the efferent neurons of nn. V, VII, IX and X. This is the condition strongly suggested in cyclostomes. In elasmobranchs, however, and uniformly in all vertebrates of more advanced organization, the nucleus of V has separated from the remainder of the column. This is not surprising, in that the trigeminal field is the first to relinquish essentially branchial function in favor of other uses. One would expect the nucleus of VII to be the next exhibiting such a tendency, and such is the case. In elasmobranchs, dipnoans, and some teleosts the nucleus of VII still is essentially continuous with the IX-X column, but in other teleosts different degrees of specialization are exhibited. Thus the facial nucleus may partially (*Tinca*) or completely (*Silurus*) split off from that of IX-X and migrate ventrally. In others (*Gadus*, *Lophius*) there may be close connection of a part of VII with IX, these two separating from X. In this event the nucleus of VII may split into two parts, one of which remains distinct (*Gadus*).

It is generally believed that in most fish the motor cells of X lie exclusively in the vagus motor column. There is some evidence, however, suggesting that emerging X fibers do not always arise solely from the region generally regarded as visceral motor. Thus in certain teleostomes X may be reinforced internally by fibers arising from the somatic motor region of the medulla (Haller, Kingsbury, Addens).

Addens seems to base his argument for the somatic derivation of XI chiefly on the occurrence of this supposed somatic component in three genera of bony fish (*Gasterosteus*, *Spinachia*, *Ophiocephalus*), although he found that it was absent in many other forms. In these three he detected, in the region just caudal to the calamus, a bundle of fibers arising from the spinal (somatic) motor column and joining those of X internally. There is no reason, however, for assuming that this fiber bundle represents a somatic component, much less that it is the homologue of a spinal XI, as Addens does. The bony fish are very highly specialized in a number of features, and at the present time it seems more logical to consider this fiber bundle as an actual component of X, whose cell-bodies, for some reason, have split from the main nucleus and migrated ventrally, just as have the neurons that form the nucleus ambiguus of amniotes (vide infra). Indeed, Haller (1897), who found similar fibers in *Salmo*, considered their cell-bodies as an actual part of the X complex (his ventral X nucleus). Kingsbury (1897), furthermore, also encountered "ventral horn" fibers reinforcing X in *Amia*, but he appeared to have been uncertain whether they actually belonged to cells lying in the somatic motor region. This point cannot be settled without experimental or embryological investigation. It is to be noted that Addens places much reliance upon a distinction between

visceral and somatic (spinal) regions of the medulla in his interpretation of the vagus bundle under discussion (pp. 338–340), while at the same time (p. 347) he attacks the distinction between somatic and visceral nerves as being "too schematic and open to criticism."

In some amphibians (*Triton*) the primitive arrangement of a continuous VII-IX-X column still persists, while in *Rana*, possibly reflecting the higher specialization of the Salientia, the nuclei of both VII and IX are completely separable from that of X.

In reptiles the nucleus of IX has migrated ventral to the X column and in this class, and in birds, remains distinct. In turtles for the first time there is initiated a ventral X nucleus in that there is a ventral bulge of a part of the original, dorsal X column. This becomes separated in some reptiles, such as the Crocodilia and *Varanus*. It constitutes a nucleus ambiguus of sorts, but according to Kappers (1920) this structure in reptiles represents only the posterior third of the nucleus ambiguus of mammals. This is not the locus of origin of spinal XI, as will be discussed later. It should be mentioned that in birds, according to Addens, the ventral nucleus of X (nucleus ambiguus) is of dual origin, for its caudal portion includes somatic motor elements derived ontogenetically from the nucleus of XII. This appears to be a specialization peculiar to birds.

In mammals a definite nucleus ambiguus always can be identified. In *Ornithorhynchus* it is poorly developed, being a small structure that can be clearly recognized only at the caudal limit of the nucleus vagus (Hines, 1929). It thus is more representative of conditions in reptiles than in therian mammals. On the other hand, according to Kappers, the second member of the Monotremata, *Echidna*, has a well developed nucleus ambiguus, composed of both IX cells and ventrally migrated X elements. Hence in this animal the nucleus ambiguus apparently is quite comparable to the structure of the same name in therian mammals. The more recent investigations of Abbie (1934), however, indicate that in *Echidna* the development of this nucleus, particularly of its caudal portion, is less extensive than in placental mammals. The somatic motor element of X, described for *Echidna* by Abbie, which arises from an imperfectly separated portion of the nucleus of XII, is suggestive of the conditions reported in birds and some teleostomes. This detail is rather surprising, but it cannot be settled except by embryological and experimental studies. Conditions in the opossum (*Didelphis virginiana*) apparently are comparable to those obtaining in *Echidna* (cf. Voris and Hoerr, 1932), except that a supposed somatic motor component of X does not occur.

In general, it may be said that both marsupials and placentals possess a distinct dorsal motor nucleus that involves only X, its myological implication being with the smooth muscles of the viscera. This, accordingly, is general visceral efferent and parasympathetic in relationship. In addition, there is a more ventral, motor, nucleus ambiguus containing neurons implicated solely with the striated, branchiomeric musculature that is supplied by IX and X. This, therefore, is special visceral efferent. In other words, the nucleus ambiguus contains the motoneurons of the striated pharyngeal and laryngeal musculature, and therefore it is not surprising that these cells should be separated from those controlling smooth muscle.

It generally has been considered that in reptiles, as in Anamnia, the nucleus of origin of the spinal XI component is

located in the caudal end of the dorsal X column. Beccari, however, has claimed that in *Lacerta* at least it originates from ventral horn cells, and Addens that in crocodiles (and birds) the nucleus of XI occurs as a distinct caudal continuation of that of XII; hence these investigators believed these cells to have been derived from somatic efferent elements. If the cells in question actually belong to XI—a hypothesis which is far from proven, however—the mere fact of their being situated at this level is no proof of their derivation from the somatic motor column, for they doubtless have experienced stimuli similar to those influential in the descent of the cells that constitute the nucleus ambiguus. It is significant, moreover, that the investigations of both Kappers (1912, 1920) and Black (1920) in no wise support the above hypothesis of Beccari and Addens. Neither of the former authors speaks of a separate XI nucleus, but rather, in all investigated reptiles with limbs, they found a definite prolongation of the dorsal X column into the cervical region (*Damonia*, *Chelone*, *Alligator*, *Varanus*). In the apodial Serpentes (as *Boa*), in which a spinal accessory nerve is absent, such a cervical extension also is lacking, and the dorsal nucleus of X accordingly terminates abruptly in the lower medulla.

Kappers (1920), indeed, went so far as to state that there are a number of reasons for regarding the above cervical extension of the dorsal X column of reptiles as a true accessory nucleus. Furthermore, he found the relations of these cells to be extremely similar to those of the spinal XI nucleus in embryo sheep.

In addition, Lubosch (1899) stated that the spinal vagus (or XI) nucleus in Sauropsida occupies the dorsolateral part of the ventral horn, distinct from the more medial cell column homologous with the nucleus of XII, this being in contrast to the claims of Addens.

A point about which there has been much controversy is that respecting the location of the motor cells that contribute to the accessory nerve of mammals. Opinions may be divided into three schools of thought. One (a) considers that the so-called bulbar part of XI arises from both the nucleus ambiguus and the dorsal nucleus of X (as Ranson, Addens). A second thesis (b) is that bulbar XI arises exclusively from the dorsal nucleus of X and thus should be considered as but a part of the vagus proper (Black, 1914; Kappers, 1920). A third (c) denies any relationship of XI with X, in man at least, but claims that bulbar XI arises from cells in direct continuity with those of spinal XI, and therefore that bulbar XI (ramus internus) and spinal XI (ramus externus) are parts of the same nerve (Darkschewitsch, Grabower).

It seems unnecessary here to review in detail all the evidence applicable to the above points, and the matter, furthermore, cannot be settled at the present stage of our knowledge. It now appears likely, however, that Lubosch, Black, Chase and Ranson, Kappers and Addens are correct in claiming that bulbar XI is actually an intrinsic part of X, and thus that the accessory nerve (XI) comprises the spinal component only. This, however, does not mean that spinal XI is unrelated to the vagus complex, but rather that it represents a later phylogenetic development that has secondarily become more or less independent of the cranial branchial cells.

Regarding the cells of spinal XI, it is generally agreed that they are located somewhere in the lateral part of the ventral horn of the spinal cord (Black, Clarke, Darkschewitsch, Dees, Van Gehuchten, Kappers, Kölliker, Lubosch, Ranson,

Roller, Vermeulen, Waldeyer), and that they constitute a more or less distinct nucleus. Addens (1933), however, has claimed that the nucleus of spinal XI "is but imperfectly separated from the rest of the cervical motor column" in most mammals. According to Bruce (1901), the nucleus of spinal XI in man gradually changes from a ventromedial location in the upper cervical region to a more dorsolateral situation in the middle cervical segments.

In connection with the above point, we cut aseptically, under ether anaesthesia, branches of the spinal accessory nerve innervating m. trapezius of a cat. After 16 days the animal was killed, verification of the operative procedure determined by autopsy, and the cervical part of the cord fixed by injection with 95 per cent alcohol. It was embedded in paraffin, sectioned at 10 micra, and stained with gallocyanin in accordance with the method of Einarson (1932). Cells showing undoubted degenerative changes were found in the dorsolateral part of the ventral horn in a locus that is practically a direct cranial projection of the intermediolateral column of the thoracic region. Thus, in this animal at least, the nucleus of spinal XI in the middle cervical region occupies that portion of the gray matter that commonly is regarded as visceral efferent. It might further be mentioned that these affected cells were smaller than the ordinary cells of the ventral horn, a circumstance that also attests, although not conclusively, to their visceral character.

Kappers (1920) has considered the nucleus of spinal XI as being derived directly from a part of the dorsal X column, by caudo-ventro-lateral migration, and not as a caudal prolongation of the nucleus ambiguus. The close association of the nucleus spinalis XI and the nucleus ambiguus, which occurs in some mammals, he regarded as a secondary, and not a primary development. In support of this contention he cited his studies of sheep embryos and those of Vermeulen (1918). The latter found in a number of ungulates and a cetacean (*Phocaena*) that the nucleus spinalis XI was connected with the dorsal nucleus of X. Like Kappers, Vermeulen regarded these observations as indicative of the vagal origin of spinal XI. Addens, however, discarded Vermeulen's findings as a misinterpretation—an action which we regard as unjustifiable. The proximity of the more cranial part of the spinal XI nucleus to the ventromedial ventral horn cells, as described by Bruce, might well be explained by its ventral migration to form a secondary alignment with the previously descended nucleus ambiguus in accordance with neurobiotactic principles.

We consider that not a great deal can be told from the precise position of emergence of the rootlets of spinal XI, although Lubosch (1899) laid great emphasis on this point. It does seem to us, however, that their general situation between the dorsal and ventral cervical roots, both internally and externally, is strongly suggestive of a non-somatic origin.

In summary, it now appears likely that the nucleus of spinal XI has been formed by the caudal migration of original visceral (X) components, although the probability that these have been supplemented by local accretions of additional visceral elements in the cord cannot be denied. The point to be emphasized is that the nucleus of XI appears to be entirely of visceral derivation.

SENSORY NUCLEI

The only sensory nuclei that concern us here are those related to the tractus solitarius. The early homologue of the nucleus of the tractus solitarius probably

consists of the nucleus lobi vagi of cyclostomes. A predominatingly descending character of the IX-X part of this tract is encountered for the first time in amphibians, this evidently being due not to any neurobiotactic influence of the gustatory centers, but probably to visceral correlation of tongue and respiratory innervation (Kappers, 1914). In all vertebrates the nucleus of the tractus solitarius appears to be the chief—if not the sole—center for reception of the visceral afferent impulses carried by nn. VII, IX, and X. In mammals at least the nuclei related to the sensory fibers of the lower branchial nerves have experienced complication. Thus, in addition to the nucleus of the tractus solitarius itself, fibers of IX and X end in relation to other cell-groups, comprising the nucleus parasolitarius, the nucleus intercalatus, and the dorsal sensory nucleus of X. The internal relationship of the sensory components of the lower branchial nerves, therefore, is much more complex than in lower vertebrates. Much experimental work remains to be done before the exact nature of the fibers ending in these several nuclei is definitely known. At any rate, the significant fact in the present discussion is that if the spinal accessory nerve be of visceral derivation, any afferent fibers which it carries might be expected to enter the tractus solitarius, if not to terminate directly in the nucleus of this tract.

In this connection the observations of Windle (1931a) on the neurofibrillar development of the spinal cord in the cat appear to be of great significance. He found that in his smallest embryos (10 mm.), fibers forming a part of spinal XI roots could be traced into the tractus solitarius in the medulla. These were more conspicuous in large embryos, in which they were supplemented by dorsal root fibers also traceable to the tractus solitarius. That both sets of fibers probably are afferents (possibly proprioceptive) from mm. trapezius and sternocleidomastoideus is strongly suggested by the investigations of Windle (1931b) on rhesus monkeys and cats, and by those of Ranson, Davenport and Doles (1932) on cats. These indicate the likelihood that afferents from the two muscles mentioned can enter the cord (1) in direct association with the emerging motor fibers of spinal XI, or (2) directly with the cervical nerve branches to the two muscles, or (3) through the upper dorsal cervical roots by means of anastomosis with XI.

Hinsey and Corbin (1934) found evidence indicating that at least proprioceptive fibers did not follow route 3 in any of the 16 cats which they studied, but of course it is possible that they may do so in those forms in which XI-cervical anastomoses are known to occur not infrequently (vide infra).

Available data thus clearly indicate that afferents from the trapezius sheet reach the tractus solitarius, a circumstance strongly supportive of the thesis that spinal XI and its musculature are of visceral origin. It also appears beyond question that afferent fibers shift from an accessory to a spinal pathway during phylogeny. If spinal XI is of somatic origin it is difficult to understand why the afferent fibers would first have changed to a visceral (X) pathway, only later to shift to spinal nerves.

GANGLIA

In the present investigation the question of the ganglia of the nerves concerned is of considerable importance. These ganglia are of two kinds, comprising the so-called root ganglia (somatic sensory) and the trunk ganglia (visceral sensory).

Basically, nn. VII, IX and X have both

types of ganglia. In amphibians they are present, but in living reptiles, with specialized, relatively insensitive integument, the somatic sensory elements of these nerves have been lost. In mammals there are somatic sensory fibers coming from the region of the outer ear, with their cells located in the geniculate ganglion of VII (much reduced but believed still to be represented in at least some mammals), ganglion superius of IX (not always separable from g. petrosum), and ganglion jugulare of X. The trunk ganglia contain the visceral sensory neurons, and when separable they occur in a more peripheral situation than the root ganglia. These cells are located in ganglion geniculi of VII, ganglion petrosum of IX (sometimes absent in reptiles), and ganglion nodosum of X (always present, Willard, 1915).

The basic distinctiveness of these several ganglia is not conclusively established. Streeter (1905) has shown that in an early embryonic stage they are diffuse and either poorly separated or confluent. At least there appears to be no necessity for the supposition that somatic sensory neurons must separate from visceral sensory neurons, for both occur together in spinal ganglia.

An important question that here intrudes involves the position and character of the ganglion cells of the accessory nerve. In fish and amphibians the branches to the trapezius muscle leave the vagus complex peripheral to the trunk ganglion. Hence, sensory neurons of the accessory component might be located in either root or trunk ganglion of the vagus. In reptiles the accessory branches appear regularly to leave the vagus between the root and trunk ganglia. Hence no accessory neurons can occur in the latter ganglion. In mammals, however, the spinal accessory nerve has nothing to do with either ganglion of the vagus; and therefore any sensory neurons associated with it must have shifted from either or both of the vagus ganglia to some other position.

Embryological evidence for mammals indicates quite clearly that these accessory sensory cells at first are located at the roots of the spinal XI filaments. Dohrn (1901) and Streeter (1905) believed them to be continuous with the spinal ganglion crest, while Froriep (1901) considered the two to be distinct, but overlapping, entities. In either event they could well be either somatic sensory, or visceral sensory components which had migrated somewhat centrally, or both. In addition to the root ganglia of XI in embryos, it has been shown by Barratt (1899), Lubosch (1901), Weigner (1901), Fahmy (1927), Windle (1931b), and others that in some mammals (including man), at various stages of growth, there are small extracranial ganglia in XI, as well as scattered ganglion cells throughout the trunks of both X and XI. These cells were found to be more numerous in very young individuals than in adults (Fahmy).

In adult mammals it is the rule that the spinal accessory nerve has no ganglia of sufficient size to be grossly apparent, and the question naturally arises as to what has become of the afferent XI cells during phylogeny or ontogeny. Kazzander (1891), Beck (1895–96), Lubosch (1899), Weigner (1901) and Streeter (1905) have shown that there frequently occurs an anastomosis between the dorsal root of the first one or two spinal nerves and the adjacent part of the accessory nerve. The embryological investigations of Streeter indicate quite clearly that at least many of the original ganglion cells of XI become incorporated with dorsal root ganglia of cervical nerves. Evidently, therefore, there is a marked tendency for sensory cells of XI to shift over to the spinal nerves. That such migration usually is incomplete

is, however, evidenced by the not infrequent anastomosis of the accessory with cervical nerves, and by the presence in various mammals of scattered ganglion cells along the course of XI.

DERIVATION OF THE SPINAL ACCESSORY FIELD MUSCULATURE

If it could be demonstrated whether the trapezius sheet of musculature has visceral or somatic origin the fact would be of the utmost importance in the present investigation. In support of the latter thesis Addens advanced the claim of Völker (1908, not seen) that in a gull (*Larus ridibundus*) m. trapezius arises from the myotomes; and that of Favaro (1903), who stated that this also is the case in the sheep. Edgeworth (1935), however, found that in the above species of *Larus*, as well as in other birds, there is no m. cucullaris (trapezius), but that the muscle (craniocervicalis) which Völker mistook for that branchial element is derived from occipital myotomes. Hence the two muscles in question are in no wise homologous. Thus Völker's statements on this point are not pertinent to the present problem.

On the other hand Lewis (in Keibel and Mall, 1910) found in man that the trapezius first (7 mm. embryos) stands more in relation to the branchial arch series of muscles than to those of myomeric derivation. Edgeworth (1911, 1926, 1935) has also found in a variety of vertebrates that the accessory field of musculature is of branchial arch origin. In view of the extensiveness of Edgeworth's investigations great emphasis should be accorded his conclusions. The contrary and isolated claim of Favaro is in need of verification.

Further light perhaps can be thrown on this question by a consideration of the proprioceptive nerve-endings. As is well known (see Hinsey, 1934), somatic muscles regularly (but not invariably) possess muscle spindles. On the other hand, spindles are not supposed to be characteristic of visceral musculature (Hines, 1930); yet it is evident that in particular cases the latter can possess these structures, for they have been found sparingly in the masticatory muscles of rabbit (Cipollone, 1897) and pig (Cuajunco, in Hines, 1927). Furthermore, muscle spindles seem to occur in greater numbers in muscles of the limbs than in those of trunk, head and neck (Hinsey, 1934), and it has been concluded that their presence, therefore, is correlated with the diversity of use and range of activity of the muscles concerned (Hines, 1930). The trapezius complex, in addition to possessing appendicular attachment, is one of the most frequently used muscle components of the body, and accordingly it might be expected to have spindles regardless of its derivation. Thus while the presence of spindles would not necessarily indicate its somatic origin, absence of these structures would constitute evidence in favor of visceral derivation.

Willard and Lawrence (1933) found, experimentally, muscle spindles in m. sternocleidomastoideus of the mouse. Straus, using Cuajunco's modified Bielschowsky method, failed to find typical spindles in the normal m. trapezius of a 21-day pouch-young opossum (31 mm. C. R.) and of a fetal pig (59 mm. C. R.). The evidence on this point therefore is conflicting, and further investigations are necessary.

THE SPINAL ACCESSORY MUSCULATURE IN FISH

In the dogfish (*Squalus*)—representing the elasmobranchs—the nerve to m. trapezius is really nothing more than the largest and most posterior of the rami branchiales n. vagi, supplying segments of the gill musculature. The tra-

pezius occurs as a single division, arising from the skin and the dorsal superficial fascia over the back musculature, and inserting not only upon the shoulder girdle, but also upon the epibranchial cartilage of the last gill arch. In the latter detail it is in perfect sequence with the mm. interarcuales laterales of the other gill arches, although the latter take origin ventral to the back musculature. The conditions suggest the likelihood that the trapezius is merely a specialized, posterior division of the interarcuals.

If the latter be so, the question of the morphology is in order. As in the case of the membranous or clavicular girdle in bony fish, the cartilaginous girdle in the dogfish acts as a posterior boundary of the gill apparatus, and it is extremely likely that a part of the branchial musculature became attached to the girdle, largely for anchorage. The gill arches of living elasmobranchs, however, are morphologically incomplete, for in embryos of at least some forms there are well marked rudiments of still other branchial arches caudal to those that persist in the adult (Daniel, 1922). It accordingly appears likely that the disappearance of these posterior branchials has caused a hiatus in an originally continuous series of interarcual muscles, and that the posterior element has persisted in the form of a trapezius division, which has become specialized for the purpose of elevating and protracting the girdle.

Innervation of the trapezius sheet in elasmobranchs regularly is stated to be solely by branches of the vagus nerve, and thus Howell has found it. Nishi (1922), however, stated that in a number of selachians—but not in *Cynias*, *Alopias* and *Chimaera*—the trapezius is innervated not only by branches of the vagus, but by spinal nerves as well. He accordingly believed the muscle to be of dual origin. It is, of course, impossible to deny that some selachians may have taken the same sort of step as reptiles in this respect, but at least this needs careful proof. Howell found branches of spinal nerves passing to the deep surface of the trapezius in the dogfish. He stimulated electrically all such that he encountered, but without result, and concluded that they were cutaneous nerves, which pierced the trapezius on their way to the integument.

Cyclostomes lack pectoral fins and girdle; hence there is no m. trapezius recognizable as such. In the bony fishes, skeletal details are very different from those in elasmobranchs. Typically, in the former, the common gill opening is bordered by a circle of membranous bone, continuous above with the skull. This bony arc not only constitutes the posterior boundary of the gill apparatus, but is the clavicular girdle, so-called, with which the cartilaginous pectoral girdle has come, in higher vertebrates, to fuse. It is upon this membranous girdle that all of the extrinsic muscles, both somatic and branchial, at first insert.

In sharks the visceral muscle so attached to the girdle—the trapezius—has become a muscle for moving the girdle, and has broadened and increased in power. In bony fishes, on the other hand, no muscle can move the membranous girdle, because of its firm anchorage; hence visceral muscles that may be attached to it can move only some part of the gill apparatus, and consequently they are much weaker. In the cod (*Gadus*) Howell (1933) reported two visceral slips to the girdle, one above and one below, while in other fish there at times are additional slips. Because of the extreme specialization of teleosts it is doubtful if these visceral slips can always he homologized in diverse forms. A trapezius of sorts, with vagus innervation, has been reported for *Lophius* (Guitel),

Menidia (Herrick, 1899), *Esox* (Vetter) and others. The absence of a trapezius has been claimed for *Amiurus* (McMurrich), *Perca* (Vetter), and *Gadus* (Herrick, 1900).

There is no reason why a trapezius should not have been lost by any number of existing fish during evolution toward extreme specialization. That it may be lacking in some is readily conceded; but existing reports of its absence are not convincing. Thus Vetter stated that in *Perca* the trapezius is a somatic muscle innervated by spinal nerves, and Herrick (1900) that in *Gadus* the trapezius stretches from the cranium to the girdle and likewise is innervated by spinal nerves. Howell dissected these genera and found that the muscle which these two authors have called trapezius is obviously a division of the trunk musculature, but that small slips with vagus innervation extend from the gill structure to the membranous girdle in both forms. This causes one to suspect that when an author reports the absence of visceral muscles to the girdle in bony fishes he was looking for a broad muscle of conventional trapezius form, and has failed to detect smaller, deeper visceral slips.

Vetter (1878) reported that the trapezius in *Esox* is innervated by both nn. IX and X, but subsequently he stated that the nerve in question may have been a lateral line branch. Howell investigated the condition in this genus but could find only vagus innervation of the trapezius.

In conclusion it may be said that a representative of m. trapezius is believed to be uniformly present in fishes, although eventually it may prove to be absent in some few forms. It is innervated, so far as known, solely by a posterior twig of the series of vagus branches supplying the posterior part of the gill musculature.

THE SPINAL ACCESSORY MUSCULATURE IN AMPHIBIANS

The cranial nerves of *Amblystoma* (Herrick, 1894), and apparently other Caudata as well, are much specialized, as partly indicated by the fact that nn. IX and X constitute a single, closely-knit complex (cf. Lubosch, 1899). Their roots are in intimate relationship, and but a single, large, common ganglion is apparent. No separate n. XI is present, this being represented only by the most caudal rootlets of n. X. Likewise spinal n. 1 arises by several roots, but habitually lacks a dorsal root ganglion, which structure, however, has been reported as present in *Salamandra* (Von Plessen and Rabinovicz, 1891, not seen). This is not supposed to contribute to the hypobranchial (hypoglossal) innervation (by sp. n. 2, or 2 and 3).

In amphibians the accessory field is undivided, with no "sternocleidomastoid" differentiated. In most Caudata at least it is broad, and arises from the superficial fascia of the back, while in Salientia it appears to have a tendency to shift toward the head, and usually is thicker. It is especially narrow in the common toad and arises exclusively from the head, so that it more closely resembles a sternocleidomastoid than it does a trapezius. In urodeles it inserts at the anterior base of the scapula, and in claviculate anurans upon the acromial process. The innervation appears to be supplied solely by a branch of the vagus, although Norris (1913) reported in *Siren* that innervation was also by small "dorsal" branches of spinal nn. 1 and 2, other small branches of which supplied m. levator scapulae. It is not at all impossible that some few amphibians have initiated the step that has been taken by the reptiles, and that their trapezius also may receive spinal branches. On the other hand, it is not improbable

that the spinal nerves which Norris found going to the trapezius were actually cutaneous nerves which pierced the muscle. At least the circumstance of spinal innervation needs verification, and if found to be so it is extremely likely that the spinal branches concerned carry only sensory fibers (vide infra).

Miner (1925) reported that in the giant salamander (*Megalobatrachus*) the ventral part of m. levator scapulae, unlike the dorsal part, inserted by an aponeurosis, and that the innervation of the former included visceral fibers from n. vagus. Neither Humphry (1871) nor Osawa (1902) reported such an occurrence in this animal, and Howell could not find it in other salamanders, including *Cryptobranchus*. Hence it is likely either that the nerve twigs which Miner encountered did not actually innervate the muscle, or else that his was an abnormal specimen.

In summary, it may be said that in amphibians there always is an undivided muscle unit representing the accessory field, innervated by a branch of the vagus nerve. Possibly in some forms this musculature may receive spinal contributions, but the point needs verification.

THE SPINAL ACCESSORY MUSCULATURE IN REPTILES

In modern reptiles of lizard-like conformation the accessory field arises by aponeurosis dorsal to the girdle and from the posterior part of the cranium. It inserts upon the anterior border of the scapula above the clavicle, upon the entire length of the clavicle, and upon the interclavicle. Its history suggests that in ancient reptiles insertion was upon the length of both cleithrum and clavicle, before the former disappeared, and that it constituted *the* muscle for advancing and at the same time elevating the girdle.

Fürbringer (1900) long since demonstrated that in recent lacertilians there are encountered all stages between an undivided condition of this muscle sheet and one in which a sternocleidomastoid moiety is completely separable. In any case, the portion representing the latter usually is considerably thicker than the remainder of the muscle.

The fact that a sternocleidomastoid does not differentiate in vertebrates below the reptiles is a rather conclusive indication that the accessory field has developed from a single, dorsal, branchiomeric unit, and not from both dorsal (trapezius) and ventral (sternocleidomastoid) components, as a study of amniotes might lead one to suspect.

In living reptiles the more proximal part of X is complicated to various degrees by connection with IX, XII, and the sympathetic trunk, as discussed in the excellent paper of Willard (1915). Thus IX, X (with potential XI) and XII may form an essentially single trunk, from which a number of fine twigs diverge to the trapezius. The rootlets of X extend down into the cord, at times as far as the third cervical segment (cf. Lubosch, 1899). Occasionally it has been reported, as in *Salvator* (Fischer, 1852) and *Chelonia* (Bendz, 1843), that the most caudal vagus rootlets form a separate nerve, which undoubtedly represents a spinal XI. One can hardly doubt that any trapezius branches diverging from a cranial complex encompassing X elements are actually X (XI) components, and they have always been so reported as present except in *Chamaeleo* and *Agama* (Fischer), *Trionyx* (Ogushi), and *Anolis*. In *Anolis carolinensis*, Willard claimed that there is no cranial innervation of the trapezius. An animal of such small size is difficult to investigate grossly, and in order to determine this point we examined a large species of West Indian *Anolis* belonging to the U. S.

National Museum. In this individual X and XII anastomosed to form a stout trunk from which the trapezius sheet received innervation. It is hardly likely that this situation obtains in one species of a particular genus and not in another. In view of this, the conditions as reported in *Chamaeleo* and *Agama* by Fischer over 80 years ago need verification. Ogushi (1913) claimed that the plastro-squamosus of *Trionyx japonicus* (which he homologized with the sternocleidomastoid) is innervated solely by C_8, but it is likely that he was mistaken in interpreting this muscle as a representative of the accessory group.

In reptiles for the first time the accessory field regularly receives additional innervation by way of the spinal nerves. In both *Iguana* and *Sphenodon* at least three spinal nerves (3-5 or 4-6) are concerned. Apparently there has been but little curiosity regarding the composition of these nerve branches until the present investigation of the subject. In individuals of *Iguana*, under ether anaesthesia, Howell cut these nerves and stimulated the peripheral stumps. No action resulted, indicating that they carry no motor fibers to the accessory field of musculature. The central stumps were then stimulated. Through n. 3 there was no action, indicating that this branch carries only sensory fibers that are not stimulable under these conditions. Through the central stump of n. 4, action of the anterior (sternocleidomastoid) part of the muscle was produced, and through that of n. 5, action of the posterior trapezius. Spinal nn. 4 and 5 thus carry afferent fibers of a different type than those passing through n. 3. The former are electrically excitable under anaesthesia and elicit motor responses by way of vago-accessory branches to the muscle. In an additional, very large specimen, on the other hand, we indubitably found motor innervation of the sternocleidomastoid through n. 3, and less certainly of the trapezius through n. 4.

We also investigated these conditions in an alligator, and by stimulating the peripheral stumps of the cervical nerves, ascertained that they carried no motor fibers to the accessory field of musculature.

In the light of these experiments it accordingly seems clear that afferent fibers, which presumably at an earlier stage followed the pathway of the vagus, in reptiles have shifted so as to take a spinal route, thus making a short cut. Doubtless there is involved in this step a variety of fasciculative or neurobiotactic principles, and there may be a tendency for afferent fibers to take a pathway to their neurons by the shortest practicable route. In addition, accessory motor fibers also have adopted this new pathway in reptiles, but less constantly, as indicated by the variability of their occurrence.

THE SPINAL ACCESSORY MUSCULATURE IN MAMMALS

In mammals the accessory field of musculature always is present. Except in Cetacea there uniformly is a m. trapezius, which usually is extensive and essentially continuous from the occiput to a level well caudal to the shoulder. Not infrequently this is partially separable into portions inserting upon scapular spine, acromion, and clavicle. In monotremes, however, there are two well separated portions, one chiefly from the head, the other from the dorsum of the thoracic region. A part representing a sternocleidomastoid always is present, even in Cetacea, occasionally (Monotremata) partially covered by the trapezius. There may be separate slips of origin from sternum and clavicle, and separate insertions upon mastoid and occiput, so that sternomastoid, sterno-

occipital, cleidomastoid, and cleido-occipital portions are distinguishable.

Innervation of both muscle divisions always is by both spinal accessory and cervical nerves except in certain long-necked ungulates. We have not encountered any contribution from C1, but this may well occur as an exception. Usually the spinal innervation comes from C2, C3, and C4, in part or in whole, either as branches from the single roots (as in the rule in the dog), or as branches, each of which is derived from components of adjoining roots, C2-C3, or C3-C4 (as in man). In man, if the spinal innervation of the accessory field be contributed by C2-C3, the branch frequently will join the trunk of XI, while if it comes from C3-C4 it usually follows a separate course. A partial exception to the above generalizations is encountered among long-necked ungulates (camel, llama, giraffe), in which the spinal branch of XI may be absent, the trapezius-sternomastoid complex then being supplied solely by cervical nerves (cf. Howell and Straus, 1934). In all other mammals the spinal XI apparently is present, and extends for various distances down the cord (cf. Lubosch, 1899).

In this connection it is important to know what the above-mentioned cervical branches carry in mammals. Are they purely sensory as sometimes in reptiles, or have motor fibers begun to follow this route, and to what extent? Several authors have endeavored to answer these questions.

Chauveau (1891) found in horses that m. sternomastoid was innervated by a nerve trunk formed by junction of XI with C2. Apparently using no anaesthesia, he demonstrated that pain fibers from this muscle were carried only by C2, a conclusion in entire agreement with the results obtained on cats by Windle and DeLozier (1932). Chauveau also found that the spinal contribution to the sternomastoid carried no motor fibers, but apparently contained afferent fibers in addition to those concerned with pain. Thus stimulation of the central stump of the C2 branch, with XI intact, produced contraction of the sternomastoid. All motor fibers to the sternomastoid in the horse accordingly are carried by XI. Chauveau's investigations did not include the trapezius. As far as the sternomastoid is concerned, however, its innervation is of a relatively primitive type, in contrast to the extreme condition occurring in long-necked artiodactyls, in which there is a tendency for not only the sensory but also the motor fibers completely to shift from XI to spinal nerves, so that the former nerve may entirely disappear.

Lesbre and Maignon (1908) repeated the experiments of Chauveau on horses, a cow, and dogs. They concluded that the motor supply of the trapezius-sternocleidomastoid complex in the two ungulates is entirely through the accessory nerve, whereas the cervical supply is purely sensory. Their statements concerning the dog are not entirely clear, but suggest to us that a cervical motor innervation may have been encountered. The observations of Todd (1912) on ungulates appear to confirm the conclusions reported above.

Sternberg (1898) found in the macaque that the cervical contribution to the sternomastoid carried no motor fibers, but that the trapezius, on the other hand, did receive efferents by this route. In contrast to this, however, both Russell (1897) and Sherrington (1898) encountered cervical motor innervation of both muscles in this animal. Sternberg repeated Russell's work and reached the conclusion that the latter's result with the sternomastoid was attributable to spread of electrical current from the cervical roots to the adja-

cent XI. From our experience with dogs we deem it likely that the discrepancy between these reports in large part may be explained by individual variability of the animals studied.

In an effort to settle some of the points at issue we undertook to investigate, under ether anaesthesia, the innervation of mm. trapezius and sternocleidomastoideus (divisible into two distinct parts) in a series of dogs that had already been used, mostly in experiments on the cerebrospinal fluid. At first we employed the Harvard induction coil as a source of faradic current, but found this so unsatisfactory that we devised another apparatus that would furnish current of measured voltage with a sine wave current of 60 cycles. Thirty dogs were investigated, but seven of the experiments were discarded for reasons such as the following: in five instances the accidental sectioning of nerves, or the death of the animal before entire completion of the experiment; and in two cases the entire absence of action of the accessory field of musculature following stimulation of *either* stump of all the sectioned cervical nerves. The elimination of these last experiments may be unjustified, because the cervical nerves actually may have contained neither efferent nor electrically stimulable afferent fibers for this field. We have preferred, however, as a more conservative policy, to exclude these animals from our tabulations. Thus in the 23 animals included in table 1 all showed action of the accessory field musculature following stimulation of *either* the peripheral or central stumps of at least one of the sectioned upper cervical nerves. Even in this series it has been virtually impossible to be certain that no fine nerve twigs have been broken, or that all of them have been detected. Nor could it always definitely be ascertained whether C4 did or did not reach the musculature under consideration. The discrepancy in numbers of experiments listed in table 1 (as 20, 21, or 22) is attributable to several factors. Thus in two animals C3 apparently failed to innervate either m. sternocleidomastoid or m. trapezius, while in others there were such adventitious reasons as loss of a nerve stump following slipping of a knot. For these reasons, therefore, we prefer to regard the results in these particulars as tentative rather than conclusive.

TABLE 1

Results of electrical stimulation of cervical nerves supplying the accessory field of musculature in dogs

The first figure in each column indicates the number of animals in which muscular action was so secured, the second figure the total number of animals considered.

	N. 2	N. 3	N. 4
Peripheral n. stump			
Stern. cl. mast.	12/22	3/21	0/8
Trapezius	5/21	6/20	3/8
Central n. stump			
Stern. cl. mast.	10/21	8/21	3/8
Trapezius	0/20	5/20	0/8

The technique employed was to expose the cervical branches which supplied the accessory field and to stimulate them with a unipolar electrode. Threads were then tied to two points on each branch and the latter sectioned between the knots. The peripheral stumps were then stimulated. If action of the accessory field could be secured at all, it followed application usually of less than one-quarter, or at most one-half volt, thus establishing the presence of motor fibers. The central stumps were then stimulated. If any action followed, a current in the neighborhood of one volt was required. Such action indicated that—as in reptiles—the nerves carried stimulable afferent fibers connected with efferents of the accessory nerve, for muscular contraction resulted

even after all other pathways to the accessory field had been interrupted.

The character of these excitable afferent fibers does not concern us here, but merely that they were afferents connected with motor fibers to the accessory field, reaching the muscles by a pathway (XI) other than by the spinal nerves. The possibility must be entertained that a few of the results obtained by stimulating central stumps may have been due to axon reflexes. We were careful, however, to destroy the infrequent proximal connections between neighboring spinal nerves, and it is unlikely that axon reflexes obscured the results in more than a very small minority of cases, if at all.

From table 1 it is apparent that the sternocleidomastoid generally receives a more cranial cervical motor innervation than does the trapezius, with diminution caudalward, and that C4 does not, in our experience, so contribute. The cervical motor fibers to the trapezius, on the other hand, may reach the muscle via any of the three nerves mentioned.

Motor fibers, determined by stimulation of the peripheral stumps, were carried to some part of the accessory field by C2 in 13 out of 21 complete experiments, but only in 3 of these animals to both mm. sternocleidomastoideus and trapezius; by C3 in 8 out of 20, but in only one instance to both muscles; and by C4 in 3 out of 8, but never to both muscles. In those dogs in which both C2 and C3 were completely investigated, at least one of these nerves carried motor fibers to one or both of the muscles under consideration in 15 out of 21 instances. In 6 out of 21 animals motor fibers were carried by both C2 and C3. Complete absence of cervical motor fibers was exhibited by 5 animals.

As with the motor innervation, stimulable afferent fibers with sternocleidomastoid connection have been found most frequently to be carried by C2, but in contrast to the efferents these not infrequently are present in C4. Stimulable afferents of the trapezius, however, were detected only in C3. In this connection it is of interest to note that these fibers are distributed to the motor mechanism of the sternocleidomastoid broadly over three cervical nerves, whereas those concerned with the trapezius in our experience are confined to a single cervical pathway, and are present less frequently. It also should be noted that stimulation of the central stumps of these cervical nerves usually resulted in marked increase of respiration.

Stimulable afferents, concerned with some part of the accessory musculature, were carried by C2 in 9 out of 10 complete experiments, but never to both muscles; by C3 in 10 out of 20, but only in 2 instances to both muscles; and by C4 in 3 out of 8, but in no instance to both muscles. In the 18 cases in which both C2 and C3 reached this field, stimulable afferent fibers concerned with either or both of the muscles in question were carried by these nerves in 13 instances; but only in 3 of them were these fibers detected in both nerves.

We investigated the same features of a chimpanzee, again using ether anaesthesia. Innervation of the accessory field was by XI and a spinal branch derived from both C3 and C4. This branch was cut. Stimulation of its peripheral stump resulted in weak though definite action of the trapezius, and the same result, though in stronger degree, followed stimulation of the central stump. This shows that in this animal spinal nerves carry motor fibers to the XI field, and also stimulable afferents to the XI motoneurons.

If any of the motoneurons of the accessory field are of somatic derivation, these, whose axons follow a spinal nerve path-

way, might be expected to be the ones. Our attempts to investigate this point by experimental procedure thus far have been entirely inconclusive.

Our experiments indicate that in reptiles both afferent and efferent fibers from the accessory field for the first time have shifted over from vagus branches representing an accessory nerve to a spinal nerve pathway. In mammals the step probably is carried farther. An apparently larger proportion of motor fibers have adopted the spinal nerve course. The pattern of distribution of these motor fibers seems still unfixed, for they exhibit much variability.

The evidence suggests that afferent fibers are less conservative in the route of their distribution than are efferent fibers, and to some extent have a tendency to adopt short cuts, when such are feasible. A new afferent pathway having become established, the corresponding efferent fibers may finally come to take the same route, following the afferents according to the principle of fasciculation, as expounded by Kappers (1932).

Because the accessory field of musculature in anamniotes is innervated solely by visceral, and in amniotes by both visceral and spinal components, it frequently is assumed that in the latter group a new myological element of myomeric (somatic) origin has been added. In view of the evidence that has been presented here, it appears that such an assumption no longer is tenable; for if our interpretation be correct, the spinal branches to the trapezius complex constitute nothing more than visceral (branchial) components that have shifted so as to follow a spinal pathway.

CONCLUSIONS

The spinal XI nerve is to be regarded as a derivative of the vagus complex, and hence, of visceral origin. Support of this conclusion is found in the phylogeny of its motor nucleus, which evidently has been derived from the dorsal motor nucleus of X by caudoventral migration, and in the apparent course of the afferent fibers from its musculature into the tractus solitarius, an undoubted visceral sensory pathway.

Although originally a mixed nerve, with ganglion cells primarily associated with those of X, it exhibits a strong phylogenetic inclination to lose its sensory cells, by their migration onto the dorsal roots of adjacent cervical nerves. The motor fibers appear to be somewhat more conservative, but eventually they also tend to follow this new and shorter spinal pathway, and hence, to become ensheathed with emerging cervical fibers according to the principles of fasciculation. This is carried to an extreme in long-necked ungulates, in which the spinal accessory nerve tends to disappear as a gross entity. As a result, the nerve fibers of the musculature concerned come, in amniotes, to follow two separate pathways.

The stimuli for the formation of a spinal n. XI of characteristic form are obscure. It is not improbable that these involve neurobiotactic influences, among which may be suggested the constant cofunctioning of this muscular field with somatic muscles of cervical innervation, the phylogenetic descent of the shoulder, and the important rôle that the trapezius and sternocleidomastoid have come to play in respiration.

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THE NUTRITIONAL REQUIREMENTS OF BACTERIA

By WILLIAM BURROWS

Department of Biostatistics and Department of Biology, School of Hygiene and Public Health, the Johns Hopkins University

THE problem of the nature and extent to which the growth of organisms is influenced by kinds of food substances available to them is one of fundamental importance in biology. The biologist has been interested in this problem not only as it concerns the higher plants and animals, but also in connection with the growth and reproduction of unicellular microorganisms—bacteria, yeasts and protozoa. The bacteriologist has been peculiarly and particularly involved in this phase of bacterial activity since a great part of his experimental work is possible only through his ability to grow these microorganisms on the so-called artificial or laboratory media. We may recall the second of Koch's postulates, *i.e.*, the organism of suspected etiological significance must be *grown* in pure culture (author's italics). This premise has been used again and again in all kinds of bacteriological work by substituting for "etiological significance" some other appropriate phrase such as "nitrogen fixing ability."

For many years, in fact since the early fermentation experiments of Pasteur (1860), microbiologists have sporadically investigated the nutritive requirements of bacteria and other unicellular organisms. That the problem has been attacked in a more or less haphazard, trial and error way is amply evidenced by the compilation of literally thousands of formulae for culture media (*cf.* Levine and Schoenlein, 1930). The underlying theme of a great part of these researches has been that most bacteria and similar creatures are unable to exist on any combination of pure compounds that ingenuity can devise but must have, in greater or lesser amounts, certain preparations which presumably contain substances of an obscure nature but of great potency in their ability to stimulate growth. These hypothetical substances have been called, somewhat vaguely, growth accessory substances, vitamins, activators, biocatalyzers, bios, growth hormones and the like. Within recent years the equally vague term "essential substances" has been fashionable. The existence of these active principles has been postulated not only in connection with the growth of the unicellular microorganisms but also with that of the higher plants, insects and larvae, and higher animals. Only in this last group is there order; the individual interested in the microorganisms is subject to a chaotic deluge of observations derived from experimental work that is, in many cases, of doubtful quality (*cf.* Dart, 1934). The functions of the vitamins, hormones, certain amino acids and certain elements in the metabolism of the higher animals are relatively well known and even though in many cases the precise nature of the activity is not fully understood, the terms applied have definite meaning. Very possibly because of this, analogies have been drawn between the growth of higher animals and that of microorganisms which may or may not be warranted. The term "growth hormone" is of doubtful significance in relation to microscopic creatures; the writer, at least, is not aware

of any evidence of an endocrine system in such organisms. The human tendency to regard something that has a name as a defined entity, and a chance similarity of names as implying a relation between the hypothetical somethings is unfortunate. Lotka's (1925) quotation from H. G. Wells is particularly apropos: " . . . when we have a name we are predisposed—and sometimes it is a very vicious predisposition—to imagine forthwith something answering to the name. . . . If I say Wodget or Crump, you find yourself passing over the fact that these are nothings, . . . and trying to think what sort of a thing a Wodget or a Crump may be. You find yourself insensibly, by subtle associations of sound and ideas, giving these blank terms attributes."

The title of this paper may be interpreted in a very broad sense but the writer has chosen to take a narrow and strictly limited point of view, so far as that has been possible. We shall be concerned with bacteria for the most part and shall not refer to the great body of excellent work on other organisms except where such reference is necessary to bring out possible broad biological relationships. Again, we shall concern ourselves only with nutritional factors, *i.e.*, those *substances* which are intimately and *specifically* related to the synthesis of protoplasm; such substances may have a catalytic type of function or may serve as sources of raw material. This unsatisfactory definition obviously omits from consideration physico-chemical factors such as surface tension, temperature, hydrogen ion concentration and a host of others as well as all reference to the oxidative reactions without which synthesis could not go on. It is admittedly a highly artificial separation but one which is allowable for the purposes of the present exposition. It has been impossible to avoid stepping over those boundaries from time to time but such excursions have been kept at a minimum.

Two further definitions are necessary before we may proceed. The first of these is that of a synthetic medium. The early concept of a synthetic medium was that it should consist of inorganic salts together with some source of energy. While such a medium still remains the only type of solution in which autotrophic bacteria will flourish, the needs of the more fastidious bacteria have enlarged and broadened this original concept. The definition proposed by Burrows (1933) is fairly satisfactory at the moment, *i.e.*, "A synthetic medium may be defined as one in which all the constituents are definite chemical compounds of known composition and structure."

The other definition is that of growth. The writer prefers to regard growth as synthesis of new protoplasm and it is in that sense that the term is used here. We are primarily interested in the conversion of the constituents of a medium into more bacterial protoplasm; it is immaterial, if cellular division is not regarded as a process apart from growth, just how many and in what size packages this new protoplasm is wrapped. (At this point we come perilously close to the boundaries of our subject for surface-volume relations become of prime importance with increasing size of protoplasmic packages.) With this concept of growth, the enumeration of bacteria by plate counts or even by total microscopic counts becomes inadequate and Mueller's (1935a) method of nitrogen analyses or a similar means of estimation becomes obligatory.

We may, perhaps, diverge for a moment into a consideration of the implications of the term growth in relation to bacteria. The process, regarded as essentially proto-

plasmic synthesis, may be considered to have its beginnings in the specific catalytic mechanisms of the syntheses which result in that mixture, protoplasm. It is quite evident, particularly in the case of the bacteria, that the biological individuality of an organism is the result of the *specific* nature of such catalysis. (It may be noted here that the term catalyst is used in a very broad sense—catalytic activity may be due to "soluble" enzymes or to certain electro-chemical configurations at intracellular interfaces or whatnot.) This is obvious when one recalls that the identification of a bacterium is based on its biochemical activity, *i.e.*, its fermentations etc. and on serological reactions. The latter means of differentiation arises as a result of the antigenicity of certain protoplasmic constituents, the specific synthesis of which results in the production of a given bacterial strain. These microörganisms closely approach the ideal experimental animal for the study of the mechanisms of such syntheses for, so far as we know, they are not complicated by the integrating factors which are the inseparable companions of multicellular organization and differentiation. A somewhat shorter train of guesses is involved in connecting protoplasmic synthesis and antigenic content of a bacterium than is necessary to relate the morphology of a mammal and such synthesis.

It is no doubt apparent at this point why physico-chemical factors and the purely oxidative reactions may be provisionally left out of the present discussion of nutrition. Such influences may, in a somewhat artificial but nevertheless very real sense, be regarded for the present as non-specific. This concept of non-specificity becomes somewhat clearer with a consideration of what we have called the purely oxidative reactions. The oxidation of carbohydrates, simple organic acids, etc. is a necessary correlary to growth—a mechanism which provides energy for the use of the growing cell or, from another point of view, an oxidation coupled with the reductive processes of synthesis. The particular source of free energy is more or less immaterial as long as it remains within what one might call the realm of biological possibility. A given bacterium may oxidize glucose, formic acid, citric acid and other such compounds with equal facility or, in the absence of these, will oxidize amino acids or whatever suitable material there may be at hand. The particular substance oxidized does not, so far as is known, influence the specific nature of the new protoplasm. While some bacteria may oxidize glucose largely to butyric acid and others oxidize the same sugar to acetic acid, the process is still non-specific in that it may be used by a variety of bacteria. In other words, the particular fuel burning under the boiler does not require that the resultant energy be dissipated in the sawing of wood rather than the pumping of water.

It is probable that a variety of approaches may be made to the problems presented by this concept of growth. Burrows and Jordan (1935) (1936) (unpublished experiments) have attempted to throw some light on growth processes by a study of apparent oxidation-reduction potentials produced in cultures, with suggestive but inconclusive results. Although other modes of attack will undoubtedly present themselves, at present, study of nutritive requirements seems to offer the most encouraging outlook. The writer is not aware that the foregoing reasoning has provided the motive for the multitude of experiments on the growth requirements of bacteria. At the same time, such studies do appear to be directed, either consciously or unconsciously,

toward the ultimate elucidation of the synthetic mechanisms involved in growth.

The present paper is not intended to be a review of the voluminous literature on bacterial nutrition. The excellent reviews of Sergent (1928), Stephenson (1930), Buchanan and Fulmer (1930) and Peskett (1933) are entirely adequate. Our present knowledge of growth requirements and growth stimulation does, however, need interpretation and integration insofar as that is possible.

While at the moment it is hardly practical to attempt a segregation of "growth promoting substances" on the basis of their chemical nature, it is possible to develop a rationalization of a sort based on what is known, or what may be inferred or hypothesized, in regard to the mechanism of the effects produced. The writer ventures to suggest a tentative scheme of this nature with the hope of bringing some order into the present chaos. Four defined categories into which growth promoting activities may be distributed are proposed. These categories are:

1. *Indispensable elements.* While certain elements such as carbon, nitrogen, hydrogen, oxygen, phosphorus and many others are obviously necessary, either in combination or in the elementary form, to the growth of bacteria and other organisms, certain other elements, iron, copper, magnesium, etc. are probably necessary in traces.

2. *Growth accessory substances* or what are usually regarded as vitamin-like substances constitute a group exceedingly difficult to define. Suffice it to say that preparations presumably containing such substances are characterized by their marked activity in extremely low concentrations and by their indispensable character. The effect of these substances may be that of inducing growth which would not otherwise take place or, more often, producing a strongly stimulative effect on the scanty growth presumably resulting from inadequate amounts of the active material.

3. *Essential substances.* This group may be defined as consisting of those substances which contain certain molecular configurations which must be supplied to the organism which lacks the necessary catalytic mechanisms for the synthesis of such structures from the raw material provided. This group is distinguished from Group 2 on a quantitative basis, *i.e.*, substances included here such as amino acids, must be supplied in considerably more than traces since a definite proportion of the new protoplasm will consist of such material. A further restriction, that the structure of an essential substance must be known, serves to distinguish this group. These distinctions may eventually prove to be artificial—with complete knowledge Group 2 should merge with Group 3—but they are convenient at the moment.

4. *Growth-stimulating substances* are those substances which are not indispensable but which, because of their unusual lability to bacterial oxidative mechanisms or because of their ready conversion to suitable oxidation-reduction systems or for other reasons, produce a strongly stimulative effect on bacterial growth.

INDISPENSABLE ELEMENTS

While it is obvious that many of the common elements, often in combination, are indispensable to bacterial growth, the position of other elements usually regarded as rare, biologically speaking, is uncertain. It is reasonable to assume, however, that some of these are actually integral portions of bacterial protoplasm and must, therefore, be supplied. It is extremely difficult to provide experimental demonstration of such indispensability for necessary amounts may be so small as to defy chemical analysis and purification pro-

cedures. It may be possible in some cases to use extrapolated curves as Burk and his associates have done in connection with nitrogen fixation with Azotobacter but this is open to some criticism. A great amount of research on the oligodynamic activity of metals has shown that, whether actually indispensable or not, many of these exert pronounced growth stimulating effects in very low concentrations. Although the literature has been reviewed by Buchanan and Fulmer (1930) it is of interest to point out a few specific instances of such an effect. Bertrand (1912) has demonstrated the importance of manganese in cultures of Aspergillus. In Raulin's medium prepared as free as possible from the element, mycelial growth but no spore formation took place. The presence of as small a quantity as 0.00001 per cent stimulated growth and spore formation markedly. Javillier (1913) showed that cadmium sulfate when present in quantities of one part in 10,000,000 markedly stimulated growth of the same fungus.

The stimulating action of iron salts on the growth of the tubercle bacillus has been noted by a number of workers including Frouin and Guillaumie (1924), Henley (1925) and Long and Seibert (1926). Ruhland (1922) came to the conclusion that iron is essential to the assimilation of carbon in the form of carbon dioxide by those bacteria which oxidize molecular hydrogen. Waksman (1927) points out that "the beneficial action of humus (on the fixation of nitrogen by Azotobacter) is frequently ascribed to its inorganic constituents, particularly aluminum and silicic acid. This is confirmed by the fact that the so-called artificial humus has no such effect, while the source of the natural humus influences the degree of its beneficial action. The claim that the action of the humus is due to its inorganic constituents has been further substantiated by the fact that purified humates do not possess the stimulating effect." The recent work of Burk and his co-workers (Burk and Lineweaver, 1931; Burk, Lineweaver and Horner, 1932; Burk, 1934; Burk and Hoover, 1934) has provided convincing evidence of the importance of calcium, molybdenum, magnesium and iron in the utilization of combined nitrogen and in the fixation of molecular nitrogen by Azotobacter. These results strongly suggest an intimate relation between these metals and the catalysis of the synthesis of bacterial protoplasm from the carbon of carbon dioxide on the one hand and from molecular nitrogen on the other.

Perhaps one of the most interesting relations between an element and the growth of microörganisms is found in the importance of thallium for the growth of yeast. Gottbrecht (1880) first showed that thallium tartrate stimulated yeast fermentations and Knop (1885) later demonstrated the stimulating effect of thallium sulfate on the growth of the organisms. These observations have been verified since by a number of workers. Recently Richards (1932b) has pointed out that variation in the suitability of a synthetic medium for yeasts was in one instance due to the brand of asparagin used. The satisfactory brand proved to be contaminated with sufficient thallium for the needs of the organisms while the unsatisfactory brand did not contain this impurity. In the latter case growth was adequate when thallium was supplied. It is obvious, of course, that under these circumstances asparagin might be considered to be contaminated with a vitamin-like substance or even be essential in itself.

Mueller (1935c) has very recently shown that growth stimulating substances for the diphtheria bacillus not adsorbed on

charcoal consist of potassium and magnesium salts.

While minute traces of a variety of elements undoubtedly occur as contamination in most bacteriological media, the carefully purified material used in synthetic media may be deficient in the necessary traces of these elements. The activity of various preparations of growth promoting material may well be simply a matter of making up such deficiencies. On the other hand, even though an element is not actually indispensable it may exert a stimulating effect and thereby provide a source of growth stimulating activity. The writer suspects that the activity of many vitamin preparations may eventually be accounted for on some such basis for testing of the ash of such material has been neglected by a great many workers.

In connection with the activity of metals in bacterial growth it is appropriate to point out here that the suggestion that the growth of microörganisms, particularly yeasts, is prevented in synthetic media because of the presence of traces of toxic substances, presumably metals, was made by Chrzascz (1904) in criticism of Wildiers' (1901) work. These traces of metals are supposedly precipitated by organic matter included in non-synthetic media or by large inocula. This point has been made by other workers from time to time with regard to yeast growth although Tanner (1925) says that "in the light of recent work the metallic poison explanation seems very improbable."

Burnet's (1925) experiments with bacteria are of interest in connection with growth promoting activity and the neutralization of toxic substances. Nutrient agar plates which had been exposed to light for some time were found unfit to support the growth of staphylococci when these were inoculated in small amounts although heavy inoculations did result in growth. The inhibiting agent in the medium was found to be hydrogen peroxide and growth promoting substances active under these conditions were found to be enzyme-like substances which neutralized the growth-inhibiting properties of the peroxide. Gordon and McLeod (1926) have shown that bacterial growth may be inhibited by some amino acids in relatively high concentration. Others have observed this phenomenon in a few instances. In the writer's experience cystine is markedly toxic in concentrations near saturation at neutrality and 37°C. and the presence of large amounts of tyrosine inhibits growth somewhat. Simms (1936) has recently shown that trypsin and papain exert a stimulating effect on the growth of adult chicken tissue *in vitro* due to the destruction of a growth-inhibiting substance produced by the cells themselves.

It is questionable, however, whether growth promoting activity demonstrable under the usual laboratory conditions may be considered nothing more than the neutralization of toxic substances present in the medium. Unfavorable oxidation-reduction conditions, resulting in a bacteriostatic effect such as Burnet observed, may very possibly be of considerable importance particularly in studies of growth in synthetic media. Possible pseudo-toxic effects of this type are briefly discussed under non-specific growth stimulation.

The phenomenon of toxicity is probably of some importance in mixed cultures. McLeod and Govenlock (1921) have demonstrated the production of bactericidins by certain microörganisms and Reid (1935) has recently found that a mold produces a growth-inhibiting substance active for some bacteria. Regnier and Lambin (1934) have recently demonstrated an unfavorable effect on the

growth of staphylococci in mixed culture with *B. coli*. Volterra, in his comment on this paper, interprets such results in terms of a toxic effect and derives an integral expression from which a "coefficient of toxicity" may be calculated.

GROWTH ACCESSORY SUBSTANCES

The search for hypothetical substances, presumably of vitamin-like nature, which exert an effect on yeast growth similar to that exerted by the vitamins on the metabolism of the higher animals, has continued somewhat irregularly since the work of Wildiers (1901). He reported, it may be recalled, that the growth of yeast in a synthetic medium was dependent on the presence of an indispensable substance of unknown nature, bios. The supposition of Williams (1919) that bios was identical with undifferentiated vitamin B stimulated an immense amount of work which has been critically reviewed by Tanner (1925) and by Buchanan and Fulmer (1930). Recently Williams *et al.* (1933) have isolated a substance which they call pantothenic acid and which they and Richards (1936) have shown to be active in the stimulation of the growth of yeast in synthetic media.

Similar studies with bacteria may be said to have begun with Grassberger (1897) who demonstrated the satellite phenomenon of bacterial colony growth. The first postulation of the importance of vitamin-like substances in bacterial growth was that of Lloyd (1916) in connection with the growth of the meningococcus. Since that time literature has accumulated which has consisted for the most part of reports of the presence of growth promoting activity in a wide variety of plant and animal tissues. The literature to 1933 has been reviewed by Peskett (1933) and it is hardly possible to add to his summary. Suffice it to say that it has been definitely shown that suitable preparations of animal and vegetable tissues exhibit a marked stimulating activity in very low concentrations on the growth of some of the more fastidious bacteria. There has been disagreement as to the properties of such activities with the exception of solubility in water.

More recently Mueller *et al.* (1933) have shown that the diphtheria bacillus would grow in a solution of hydrolyzed casein which also contained tryptophane and Liebig's meat extract. Since the bacteria would not grow without meat extract, it presumably contained some growth factor of vitamin-like character. Mueller (1935b) has shown further that these bacteria required this factor when grown in amino acid solutions.

Knight and Fildes (1933) reported that a vitamin-containing preparation was necessary for the growth of Cl. sporogenes in gelatin hydrolysate solutions and Fildes and Richardson (1935) found that such vitamin material was necessary even though the basic hydrolysate medium was supplemented with certain amino acids. A study of the growth requirements of the typhoid bacillus by Fildes, Gladstone and Knight (1933) indicated that the organisms would grow in amino acid solutions but that when a purified preparation of vitamin was incorporated in the medium, several of the amino acids could be dispensed with. Although Burrows (1933) had grown *Cl. botulinum* in solutions of amino acids with no added vitamin, Fildes (1935) suggested that such positive results could be accounted for on the basis of contamination of the amino acids used with vitamin.

Allison and Hoover (1934) have found that an alcohol soluble substance from molasses and similar sources acted as a growth accessory substance in the growth of the legume nodule bacteria. In their

opinion this substance was a co-enzyme. Hughes (1932) and Knight (1935) have reported a growth factor which was necessary to the growth of certain strains of staphylococci and Sahyun *et al.* (1936) have described methods for the preparation of a growth promoting factor which not only accelerated the rate of growth of the colon bacillus but also produced an increase in maximum population.

Simms (1936) has recently shown that an "A factor" contained in blood plasma produced a reduction in the lag period and a stimulation of initial growth in adult chicken tissues growing *in vitro*. He was able to get no growth in its absence.

One of the most interesting approaches to the isolation of these active principles has been that of Koser and Saunders (1935) who have attempted to use the adsorption technique of Willstätter (1926) which has proved so fruitful in the purification of enzymes. A number of workers have noted that such growth promoting material may be adsorbed, particularly on charcoal, or, conversely, that media may be rendered unfit for supporting the growth of some bacteria by preliminary treatment with charcoal or some other adsorbing agent. Robinson and Rettger (1918) found that treatment with charcoal lowered the nutritive value of "opsine" and casein digests and Lumière (1921) showed that bios was adsorbed on Fuller's earth. The growth promoting activity for hemolytic streptococci was shown to be adsorbed on charcoal by Mueller (1922a) (1922b) and by Hosoya and Kuroya (1923) and on Fuller's earth by Funk and Friedman (1922). Miller (1924) reported that the growth stimulating properties of wort were removed by adsorption with charcoal. Factors necessary to the growth of *Streptothrix corallinus* were shown to be removed by adsorption of the medium with charcoal by Peters *et al.* (1928) and Burrows (1932) noted that the adsorption of casein hydrolysate solutions with charcoal rendered them unfit to support the growth of *Cl. botulinum*. In contrast to this experimental evidence the report of McLeod and Wyon (1921) that the addition of charcoal to the medium exerted a stimulating effect on the growth of the Shiga dysentery bacillus is of interest although it is possible that their charcoal contained impurities which possessed growth stimulating properties.

Mueller and Kapnick (1935) have recently found that the growth promoting activity for the diphtheria bacillus present in meat extract can be adsorbed on charcoal and subsequently eluted with acid alcohol. The isolation and purification of growth promoting activity by these methods has most encouraging possibilities although in view of the observations of Mueller (1934) (1935c) that certain alcohols markedly stimulate the growth of the diphtheria bacillus, the practice of elution with alcohol and acetone and with alcohol is open to possible criticism. Such successful elution is, however, in harmony with the observations of many recent workers including Walker (1922), Knight and Fildes (1933), Allison and Hoover (1934) and Sahyun *et al.* (1936) that growth promoting activities for a variety of microörganisms are soluble in alcohol and certain immiscible solvents. Tanner (1925) points out the fairly general agreement that bios is soluble in 80 per cent alcohol.

It should be pointed out here that there are several reports of preparations indistinguishable from those containing growth accessory substances, that exert a pronounced accelerating effect on carbohydrate oxidations. The existence of such an effect apart from actual growth stimulation is a point at issue in much of

the bios literature since the activity of bios preparations has at times been based on increase in numbers of cells and at others on the intensity of fermentation. *cf.* Tanner (1925). More recently Tatum, Peterson and Fred (1934) have reported that preparations made from various materials produced marked effects on the butyric acid fermentation although these same workers (1935) later showed that the stimulating effect was due to asparagin. Sahyun *et al.* (1936) showed that their "activators" produced "a great acceleration of carbohydrate consumption in synthetic media." Euler and Pettersson (1921) have shown, however, that there is apparently no fixed relation between numbers of organisms and intensity of fermentation. In their experiments a 100 per cent increase in fermentation was, at times, accompanied by only a 10 per cent increase in numbers. Such data provide support for the contention made here on theoretical grounds that such oxidations are probably not specifically related to growth processes, the availability of sufficient energy being assumed. If this condition is not fulfilled, as it may not be in some synthetic media, an increased oxidation of carbohydrate or similar material will induce an increased growth as a result of a non-specific relation between the two processes.

Naumann (1919) has pointed out that the addition of a trace of peptone, 0.0005 per cent, to an inorganic salt medium markedly stimulated the multiplication of yeasts. Other workers have pointed out this same effect particularly in connection with the digestion of crystalline proteins by some of the proteolytic bacteria. While the vitamin enthusiast will quickly point out that growth promoting activity is widely distributed in nature, the very wideness of its distribution opens the way for the suspicion that very possibly such activity is a non-specific property of a variety of organic substances rather than a property of widely distributed but *particular* substances. Hosoya and Kuroya (1923) concluded, however, that their streptococcus vitamin was different from the yeast vitamin and further that a number of amino acids tested produced no such stimulating effect. The studies of Knight (1935) appear to indicate also that some degree of specificity does exist. He has shown that a preparation active in stimulating the growth of certain pigmented races of staphylococci had no effect on the colorless varieties and that the staphylococcus vitamin was not the same as the sporogenes vitamin of Knight and Fildes (1933). The fermentation-stimulating activity of asparagin, aspartic and glutamic acids noted by Tatum, Peterson and Fred (1935) was apparently confined to the isopropyl alcohol organisms; the acetone producing bacteria were not so affected.

ESSENTIAL SUBSTANCES

The essential substances were defined above as those substances which contain certain molecular configurations which must be supplied to an organism which lacks the necessary catalytic mechanisms for the synthesis of such structures. Burrows (1933) has pointed out that "Any species of bacterium may, theoretically, be grown *in vitro* provided the proper conditions are fulfilled. . . . The most important single factor, in some cases, at least, is the chemical composition of the substrate. The question arises, in the case of the more fastidious bacteria: Just what constitutes the proper substrate? Nothing further should be necessary, from an empiric point of view, if sources of carbon and nitrogen are supplied in such forms that they are not toxic to the bacterial cell and yet are susceptible to

attack by the bacterial synthetic and catabolic mechanisms. Numerous failures to grow some bacteria on synthetic media constitute ample evidence that this does not always hold true. . . . These failures may be explained, in part, by the postulation of limits in the synthetic powers of the organisms in question." When the writer proposed this concept, together with experimental evidence which appeared to substantiate it, he had in mind particularly amino acids which, although they could not be synthesized by the organisms, were, nevertheless, integral portions of bacterial protoplasm.

Burrows (1932) and Mueller *et al.* (1933) showed that tryptophane was essential to the growth of *Cl. botulinum* and the diphtheria bacillus respectively. Burrows (1933) later showed that botulinus could be grown in amino acid solutions without tryptophane and withdrew his previous claim although according to Fildes (1935) tryptophane is actually essential to this organism. Fildes, Gladstone and Knight (1933) showed that *B. typhosus* required tryptophane in addition to a vitamin preparation although certain strains could be trained to grow without this amino acid. Fildes and Richardson (1935) later showed that certain amino acids were necessary to the growth of *Cl. sporogenes* and Mueller (1935b) (1935c) and Mueller and Kapnick (1935) similarly found that the diphtheria bacillus required certain amino acids together with preparations of growth promoting activity from meat extract. It seems rather definitely established that certain amino acids are actually essential to the growth of some bacteria. The findings have been somewhat diverse in that different species of bacteria appear to differ from one another in this respect. Burrows (1933) reported that cystine, leucine and proline were essential while lysine and glycine produced a strongly stimulative effect on the growth of *Cl. botulinum* and Fildes, Gladstone and Knight (1933) found that leucine, lysine and tryptophane were essential to *B. typhosus* although leucine and lysine could be dispensed with when "sporogenes vitamin" was supplied. Mueller's (1935b) (1935c) essential amino acids included cystine, tryptophane, glutamic acid, methionine, histidine, phenylalanine, glycine and valine (he later found that phenylalanine could be dispensed with) for his HY strain and valine, leucine, methionine and glutamic acid for the Park 8 strain. *Cf.* Mueller and Kapnick (1935). According to Fildes (1935) *Cl. botulinum* must have cystine, tyrosine, valine and tryptophane and Fildes and Richardson (1935) reported that "tryptophane, leucine, phenylalanine, tyrosine and arginine are indispensable, while histidine, cystine, methionine and valine are highly important and possibly indispensable" to the growth of *Cl. sporogenes*. These results are summarized in the accompanying table. The amino acids which have not been shown to be essential but which exert a strongly stimulative action are enclosed in parentheses.

That bacteria do differ among themselves with regard to their growth requirements, both as to essential structures and growth accessory substances is indicative of an intimate relation between such requirements and the biological individuality of the organisms. Such physiological differences in nutrition have recently been found among species of *Euglena* by Dusi (1933). *Euglena deses* will use peptones and amino acids but not ammonium or nitrate nitrogen. *E. pisciformis* will use peptones but not amino acids or nitrogen from ammonium or nitrate salts while *E. anabaena* will grow in solutions of peptones, amino acids or ammonium salts but apparently cannot

utilize nitrate nitrogen. Three other species, *E. gracilis*, *E. stellata* and *E. klebsii* grew in the presence of any of these sources of nitrogen although growth was somewhat more rapid with the organic compounds. Carrel (1931) has pointed out that ". . . has led to the discovery of strains of fibroblasts, which, although morphologically identical, differ in their nutritional properties. The food requirements of a given cell type are as fundamental a characteristic as its morphological aspect. It appears that each type demands a specific diet."

The Amino Acid Requirements of Bacteria

CL. BOTULINUM Burrows (1933)	CL. BOTULINUM Fildes (1935)	B. TYPHOSUS Fildes *et. al.* (1933)	CL. SPOROGENES Fildes *et al.* (1935)	C. DIPHTHERIA	
				HY Mueller (1935 b)	Park 8 Mueller *et al.* (1935)
(Tryptophane)	tryptophane	tryptophane	tryptophane	tryptophane	.....
cystine	cystine	.....	(cystine)	cystine	.....
leucine	.....	(leucine)	leucine	.....	leucine
.....	.....	.....	(methionine)	methionine	methionine
.....	valine	.....	(valine)	valine	valine
.....	tyrosine	.....	tyrosine	.....	.....
.....	.....	.....	(histidine)	histidine	.....
(lysine)	.....	(lysine)	.....	.....	.....
(glycine)	.....	.....	.....	glycine	.....
.....	.....	.....	.....	glutamic acid	glutamic acid
proline	.....	.....	.....	.....	.....
.....	.....	.....	arginine	.....	.....
.....	.....	.....	phenylalanine	.....	.....

GROWTH-STIMULATING SUBSTANCES

The inclusion of a group of "growth-stimulating substances" in the present discussion is hardly congruous with the emphasis that has been laid on specificity. While such a group is not justified on the theoretical basis adopted here, its inclusion is of considerable practical significance as will appear. It includes, as suggested above, only non-specific growth promoting activity, specific activity having a place in one of the other groups. It appears to the writer that it is of some importance to know whether a given growth promoting activity is specific or non-specific, for purposes of interpretation of experimental results, although such a point may seem of relatively minor significance in any particular piece of work. Such knowledge will enable us to determine whether a given activity is a general property of protoplasmic synthesis, a property of such synthesis within taxonomic groups, or, finally, whether it is concerned with the specific synthesis of specific protoplasmic constituents and therefore has bearing on what has been termed here "biological individuality."

It seems probable that much of the oligodynamic activity of metals is of a non-specific nature although in some cases a strong element of specificity is involved as, for example, in the stimulating and apparently indispensable function of thallium in yeast growth. With one or two exceptions there is little or no evidence on this point at present although no doubt such evidence will be forthcoming eventually.

Although they have been included in a "specific" group, the specific activity of

some of the vitamin preparations appears doubtful at the moment, very possibly because such preparations may consist of mixtures of active principles. The sporogenes vitamin of Fildes and his co-workers will stimulate the growth not only of *Cl. sporogenes* but also that of *Cl. botulinum* and the typhoid bacillus. Knight's (1935) staphylococcus factor stimulated the growth of a number of strains of the aureus variety. Knight feels that the properties of his factor agree closely with those of Hughes' (1932) substance. The sporogenes vitamin of Knight and Fildes (1933) appears to have some properties in common with Mueller's substance. The growth promoting activity studied by Koser and Saunders (1935) and by Koser *et al.* (1935) (1936) is apparently nonspecific in that it stimulated the growth of a variety of bacteria. Its relation to the growth factors studied by other workers is problematical. Simms' (1936) "A factor" has certain properties in common with the sporogenes vitamin, Knight's staphylococcus vitamin and Sahyun's "activator."

The stimulation of bacterial growth by definite chemical compounds has been studied by a number of workers. Wyon (1923) has pointed out the importance of amino acids as growth stimulants—an effect to be guarded against in experimental work involving vitamin-like activity (for example, the experience of Tatum, Peterson and Fred (1934) (1935).) Hosoya and Kishino (1925) and Quastel and Stephenson (1925) have demonstrated the importance of sulfhydryl compounds in the growth of obligate anaerobes and Gordon (1926) has pointed out the favorable influence of taurine on the growth of the gonococcus.

Hammet (1929) has demonstrated the stimulating effect of sulfhydryl compounds on cell division among certain of the protozoa together with the interesting observation that the oxidation products of such compounds, sulfoxide, sulfonate and sulfinate retard growth. Jahn (1933) has observed this stimulating effect of sulfhydryl on the growth of *Chilomonas* which he ascribes to an effect on oxidation-reduction potential.

It seems likely that such stimulating effects are the result of the adjustment of the apparent oxidation-reduction potential of the medium from a less to a more favorable condition. The relation between such potentials and the ability of bacteria to initiate growth has recently been of considerable interest. Aubel and Aubertin (1927), Dubos (1929a), Plotz and Geloso (1930) and others have established the importance of such potentials in the growth of certain obligate anaerobes and Knight and Fildes (1930) have determined a critical potential level above which *Cl. tetani* would not grow and below which growth was initiated. Similar studies of the facultative anaerobes have been made by Dubos (1929b) and of the obligate aerobes by Allyn and Baldwin (1930) (1932), Knaysi and Dutky (1934) and by Wood, Wood and Baldwin (1935). It has been shown by these workers and by Ingraham (1933) that a pseudo-toxic or bacteriostatic condition may exist in media in which the "toxicity" is the result of the poising action of some added compound on the potential of the medium. A variety of reducing agents will function as "growth-stimulating" substances under these conditions. Such observations are in harmony with those of Hammet with regard to the inhibiting effect of oxidized sulfur compounds and of Chambers *et al.* (1929) on the nontoxicity of dyes in the reduced form when injected into certain marine ova as contrasted with their toxicity in the oxidized state.

Burrows (1932) and Mueller (1933) found that tryptophane had a growth-stimulating effect on *Cl. botulinum* and on the diphtheria bacillus in protein hydrolysate media. Although Mueller (1935b) later showed that tryptophane was actually essential to the growth of the diphtheria bacillus, Burrows (1934) found that the function of this amino acid in the growth of botulinus was that of a non-specific growth stimulation and could be taken over by cystine. The writer has since found (unpublished experiments) that this growth-stimulating activity is also a property of suitable combinations of a sulfhydryl group with an electrically unstable carbon chain. The finding that a compound such as thiopropionamid will provide such stimulation precludes the criticism that such growth-stimulating substances may be contaminated with vitamin-like material or certain naturally occurring essential molecular structures. Mueller (1934) (1935b) has also shown that certain alcohols, notably ethyl alcohol, will, in small amounts, stimulate the growth of the diphtheria bacillus remarkably. A greatly increased growth in yeast has been obtained by many workers and most recently by Richards (1932a) when inosite was incorporated in the medium. It is difficult to understand what rôle inosite plays in the growth of yeast for apparently a great part of it is stored as such in the cells. Whether its alcoholic nature indicates anything in common with Mueller's observations is unknown.

It seems definitely established that the phenomenon of non-specific growth stimulation does exist. It is very possible that such stimulation is, in many cases, the result of marked increases in the availability of energy to the microorganisms. Sulfydryl compounds may conceivably serve as precursors of oxidation-reduction systems and thereby provide the mechanisms necessary to oxidation. Alcohols may serve as sources of energy in themselves while tryptophane is a possible source of pyrrole rings which may be necessary to the formation of certain oxidative catalysts. *cf.* Alcock's (1936) discussion.

The practical importance of the inclusion of a group of growth-stimulating substances, without regard to their possible specificity, in the tentative scheme proposed here, is apparent at this point. It is obvious that much experimental work has and will yield evidence of the existence of growth promoting activity. The thoughtless investigator will mark such activity down in the credit column of "growth hormone" or some other equally meaningless term to the inevitable confusion of his readers. If such activity may be shown to lie within or without the group of non-specific growth-stimulating substances, much will have been accomplished.

The failure of an organism to grow in a synthetic medium may be due to a variety of causes such as:

1. absence of sufficient available energy because
   a. readily oxidizable substances are not present or
   b. precursors of respiratory catalysts such as iron are not present in adequate amounts,
2. absence of sufficient nitrogen either
   a. in a non-specific but available form or
   b. in the form of essential molecular structures,
3. absence of traces of indispensable elements,
4. absence of necessary vitamin-like substances,
5. a toxic condition of the medium due either to

a. the presence of toxic substances
or
b. an unfavorable oxidation-reduction potential.

Conversely, when growth results in a synthetic medium upon the addition of some preparation it may be the result of:

1. oligodynamic activity of metals,
2. addition of indispensable elements,
3. addition of sources of energy,
4. addition of non-specific but available nitrogen,
5. non-specific growth-stimulating activity of certain compounds,
6. addition of essential molecular structures,
7. addition of vitamin-like substances or
8. an adjustment of an unfavorable oxidation-reduction potential.

No doubt lists of such possibilities can be further extended. Lest this be regarded as carrying skepticism too far, it may be pointed out that specific examples of each of these cases can be found in the literature. It is clear from these considerations that the present tendency to group all growth promoting effects under some one head is highly undesirable. Before a new type of activity is described it should be clearly defined and experimental results should be sharply scrutinized before interpretation in terms of biocatalyzers or whatnot.

CARBON DIOXIDE

The significance of partial pressures of carbon dioxide in the gaseous environment of bacteria is uncertain. While the function of the gas as a respiratory stimulant in higher animals has been adequately demonstrated, its effect on single-celled microorganisms is probably somewhat more complex. Carbon dioxide has not been included in any of the four categories proposed here for the rather good reason that it does not fit. It was shown by Wherry and Ervin (1918) that the tubercle bacillus would not grow in the complete absence of the gas. These observations were extended by a number of workers and it was found that a variety of bacteria would not grow at all or showed delayed growth when carbon dioxide was removed by absorption with alkali or washed out with CO_2-free air. It has also been definitely established that partial pressures of carbon dioxide are necessary or highly advantageous when certain species of bacteria such as brucella, the gonococcus and the meningococcus are isolated from the animal host. After cultivation on laboratory media for a time these organisms are able to grow without this special atmosphere. This literature has been comprehensively reviewed by Valley (1932) and it is hardly necessary to go into it further here. Since 1932 Walker (1932), Winslow, Walker and Sutermeister (1932), Walker, Winslow, Huntington and Mooney (1934), Walker, Winslow and Mooney (1934) and Gladstone, Fildes and Richardson (1935) have attacked the problem of the function of carbon dioxide in bacterial growth particularly in liquid media. It is generally agreed that the gas is necessary to growth of cultures, presumably its presence in the proper concentration is intimately related to cell division. Walker (1932) regards the lag phase in a bacterial culture as the time necessary for such concentrations to accumulate. Notwithstanding much investigation, however, the status of the gas in relation to the growth of some bacteria is somewhat obscure. It is uncertain as to whether it does act as a stimulant to cell division as a process apart from growth or whether it is a factor in protoplasmic synthesis or possibly both. Its function as a source of carbon in the metabolism of the autotrophic bacteria was shown many years ago by Winogradsky (1890) and is

well known at present. It is quite unlikely that it fulfills such a rôle in the experiments just cited. Carbon dioxide, therefore, seems to play at least two important parts in microbial metabolism, one rather obscure, and the other relatively well understood. Other experimental work, however, appears to indicate that it may have still other and different effects. The increased titre of staphylococcal hemolysins when cultures are grown in an atmosphere containing considerable amounts of carbon dioxide as shown by Burnet, (1929) (1930), and the pronounced effect of similar atmospheres on the formation of staphylococcal food poisoning substance in Woolpert and Dack's (1933) experiments are highly suggestive. In spite of its chemical inertness, present experimental evidence seems to indicate that it occupies a unique position in relation to the metabolism of bacteria and its relegation to a niche labelled "essential" or "growth accessory" seems somewhat inadequate.

The general scheme proposed here has all the disadvantages of every attempt to impose a semi-rigid structure on biological activity. Present paucity of knowledge of the nutritional aspects of bacterial growth, however, removes the majority of such objections at the moment and at the same time such a taxonomic approach may serve the purpose of introducing a logical element into the interpretation of the present welter of experimental data. It is purely tentative in nature and will undoubtedly be subject to considerable modification with increasing knowledge. It seems probable that the group of growth accessory substances will eventually merge with that of the essential substances. Further subdivision will, however, probably be necessary. A growth promoting activity may shorten the lag period of a bacterial culture, produce a more rapid increase in numbers, *i.e.*, shorten the generation time, or it may produce an increase in the maximum attainable population or any combination of these results. These three criteria of growth promoting activity have been used indiscriminately thus far by most workers but in the future some differentiation will have to be made and it may alter the conclusions reached here to a great extent. Such differentiation is, of course, impossible in retrospect.

While the trite remark that the line of demarcation between plants and animals runs through the bacteria has rather nebulous significance to the microbiologist, it does, nevertheless, provide a basis for the rationalization of some types of experimental work. One might venture to generalize, with an eye to the multitude of pitfalls, that the combinations of carbon, nitrogen, hydrogen, etc. satisfying the nutritional needs of plants, become more and more complex as one proceeds through the single-celled organisms to the metazoa. It is to be expected, therefore, that the type and complexity of the intramolecular configurations satisfying the growth requirements of bacteria will be extremely variable. Indeed, in view of this phylogenetic relation, if it is such, it would be surprising to find their nutritional requirements as relatively uniform as those of, for example, the mammals. That such uniformity is lacking is obvious when it is recalled that microorganisms regarded as bacteria range from the autotrophic forms to those which are designated as hemophyllic. A part of this variation is, of course, accounted for by the parasitic rôle which many bacteria assume.

On the other hand, whether the microbiologist is concerned with higher fungi,

bacteria or protozoa, it is apparent that he is dealing with protoplasm—qualitatively somewhat different perhaps, but still a substance that, regardless of its origin, has many properties in common. Certain recent work indicates that such common properties may be found in food requirements also. Tryptophane is of particular interest in this connection. The position of this substance in that group of amino acids designated as essential for the higher animals is well established. Convincing evidence of its importance in bacterial growth has been presented by a number of workers. Virtanen (1935) has recently extended the work of Kögl *et al.* (1934) and shown that β indolyl acetic acid exerts a stimulating effect on the growth of peas; a type of activity which would be placed in Group 4 of the classification presented here. It is hardly necessary in this connection to recall the position of the higher animals with regard to vitamins or that of plants in relation to auxins. Still another link between the extremes of the nutritional scale is suggested by Virtanen's (1935) observation that a prolan fraction markedly stimulated the development of certain seeds.

It seems, therefore, that, regarding the growth and synthetic mechanisms of bacteria, we may rest assured that the situation is quite as complex as that of the multicellular creatures and possibly more so. Bacteria may or may not be primitive but they are definitely not simple. While certain types of food requirements may be held in common, one may expect at the same time a great degree of diversity. The latter may be attributable not only to the intermediate position of these organisms in the biological world but also to their extreme lability and adaptiveness which, coupled with the parasitic relationship that exists in many cases, leads to a great variety of types of metabolic activity.

After the present MS was completed the monograph of Knight (Knight, B. C. J. G., Bacterial Nutrition. Material for a Comparative Physiology of Bacteria. Medical Research Council Special Report Series, No. 210, 1936) appeared. Although there are many similarities between Knight's detailed review and the condensed material presented here, the differences between the two papers appear sufficient to warrant publication of this material.

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CHARACTERS COMMON TO HIGHER PRIMATES AND CHARACTERS SPECIFIC FOR MAN (*Continued*)

By ADOLPH H. SCHULTZ

Laboratory of Physical Anthropology, Johns Hopkins University

DEGREES OF RESEMBLANCE BETWEEN THE HIGHER AND THE LOWER CATARRHINES AND BETWEEN MAN AND THE ANTHROPOID APES

Pelvis

FEW parts of the human body have undergone more profound evolutionary changes in position, shape, and proportions than the pelvis. Chiefly due to the special mechanical requirements connected with erect posture the pelvis of man has acquired a general appearance which differs very strikingly from that of the pelves of the other higher primates. In a former paper the author (1930a) has already discussed in detail many of the differences in pelvic proportions between man and, particularly, the great apes, without, however, making more than a preliminary attempt to correlate the various dimensions of the pelvis with the general size of the animal, as represented by the height of its trunk. These correlations, possible only whenever the trunk height can be measured before the preparation of the skeleton, are most instructive in trying to interpret many of the comparative data on pelvic dimensions in primates.

According to the diagrams in Figure 10, the height of the ilium in percentage relation to the height of the ischium differs comparatively little among the primates studied, with the exception of man, who is set apart by having by far the shortest ilium in proportion to the ischium. That this exceptional position of man is not due, by chance, to an unusual height of the human ischium, is proved by the third proportion in Figure 10 which shows the relation in size between the ischium and the trunk. In regard to this proportion man falls well within the range of variations among the other higher primates. The direct relation between the height of the ilium and that of the trunk (second proportion in Fig. 10) demonstrates conclusively that man is characterized among all the primates studied by the shortest ilium not only in relation to the ischium, but also in relation to the trunk. In all the anthropoid apes the ilium height—trunk height index is very much greater than in the macaque, langur, and man. A closely corresponding result was obtained by Waterman (1929), who studied the relation between the length of the iliac blade and the "length of the body" (from acetabulum to vertex) in some higher and lower primates. From the foregoing it is not surprising that the total height of the pelvis in percentage of the trunk height (fourth proportion in Fig. 10) is smaller in man than in any other higher primate and this, it can now be added, entirely on account of the shortness of the human ilium. The tremendous difference in relative height of the pelvis between man and, e.g., the gorilla is clearly shown by the exact drawings in the Figures 11, 12 and 13.

In addition to and partly on account of the shortness of the human ilium, in contrast to the ilia of anthropoid apes, the last pair of ribs reaches in man not

nearly as close to the iliac crests of the pelvis as in the great apes. For instance, in an embalmed adult chimpanzee the last pair of ribs was measured by the author to come within 40 mm. of the iliac crests and in a large male orang-utan this distance amounted to 42 mm. On the other hand, even in a negro with only 4 lumbar vertebrae and 13 pair of ribs the corresponding distance was 97 mm. This large space between thorax and pelvis in man (even larger in all lower catarrhines) facilitates lateral flexibility of the trunk. In this respect man retains the condition in the gibbon, whereas the great apes are most extremely specialized.

That the comparative shortness of the human ilium represents in general a primitive condition, in which man equals the macaque, would, in the absence of evidence to the contrary, be a more conservative conclusion than the assumption that man had at first participated in the general trend of the anthropoid apes to lengthen the ilium and had only recently experienced a secondary, very extensive shortening of his ilium. However, the lower portion of the ilium, between *acetabulum* and sacro-iliac joint is quite exceptionally short in man, as pointed out before (Schultz, 1930a, Fig. 13), so that it is justifiable to conclude that at least the caudal part of the total iliac height has become compressed and thereby shortened in human evolution after man's separation from other primates.

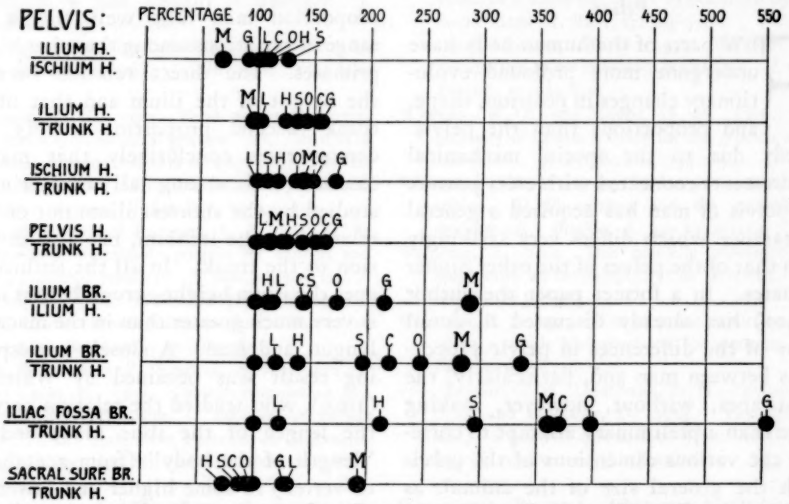
PELVIS:
PERCENTAGE 100 150 200 250 300 350 400 450 500 550
ILIUM H. / ISCHIUM H.
ILIUM H. / TRUNK H.
ISCHIUM H. / TRUNK H.
PELVIS H. / TRUNK H.
ILIUM BR. / ILIUM H.
ILIUM BR. / TRUNK H.
ILIAC FOSSA BR. / TRUNK H.
SACRAL SURF. BR. / TRUNK H.

FIG. 10. DIAGRAMMATIC REPRESENTATION OF SOME PROPORTIONS OF THE PELVIS IN HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS IN THE MACAQUE

The data for all these pelvic proportions are based upon as yet unpublished measurements by the author taken on the same adult specimens, as listed in the title of Figure 9. Abbreviations explained in title of Figure 7. Measuring technique of pelvis discussed in paper on trunk and limb skeleton by author (1930a).

As mentioned above, the width of the pelvis has become increased together with the phylogenetic widening of the trunk in general in all higher primates. The breadth of the ilium in proportion to the height of this bone is greater in the apes and man than in the lower catarrhines, as has been amply proved by Straus (1929) and by the author (1930a) and as is clearly illustrated by Figure 10 (5th proportion).

This particular index is nearly three times greater in man than in the macaque and considerably greater in man than even in any of the anthropoid apes. Since this proportion, so exceptionally high in man, refers the ilium breadth to the ilium height which has been found to be extremely low in man, it is necessary to gorilla has also the proportionately broader hips than man (see Fig. 8). The ilium breadth is really a composite dimension, determined by the development in size of its constituent parts: the iliac fossa and the sacral surface. The breadth of the iliac fossa has undergone the most far reaching evolutionary change of any

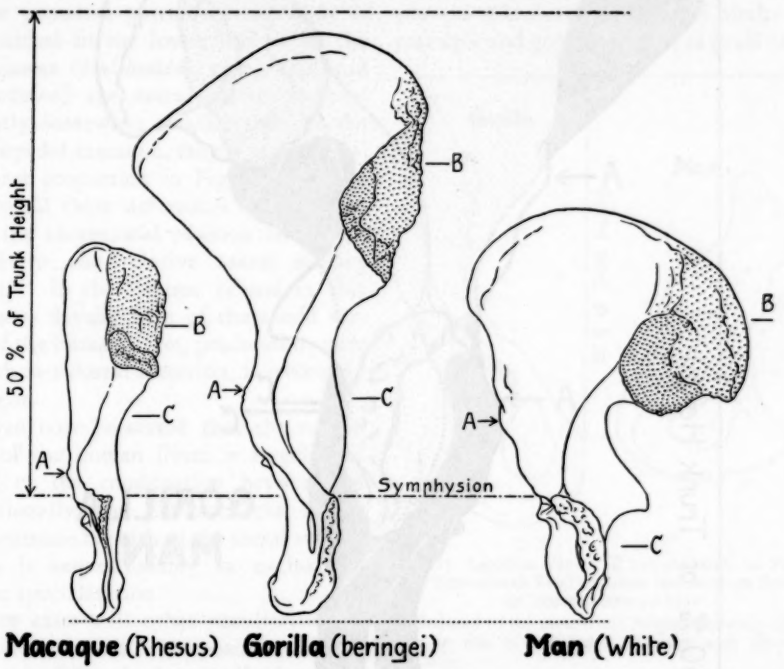

FIG. 11. MEDIAL VIEWS OF RIGHT INNOMINATE BONES OF ADULT MACAQUE, GORILLA, AND MAN
Reduced to the same trunk height, showing relative heights of pelvis and relative sizes of sacral surfaces (dotted areas). *A* = highest point on acetabulum, *B* = level of most cranial, ventral, midsagittal point of sacrum; *C* = level of most caudal, midsagittal point of sacrum. (Drawn with dioptrograph).

analyse the ilium breadth still further. By expressing this breadth first of all in percentage of the trunk height (6th proportion, Fig. 10), it becomes evident that the gorilla possesses an ilium which, in relation to the size of the trunk, is much broader than that of man and that the ilium of the orang-utan is but little narrower. It may be recalled here that the pelvic dimension in all higher primates. In percentage relation to the trunk height this breadth averages only 5.0 in the macaque, whereas 18.0 in man, 18.5 in chimpanzee, 19.9 in orang-utan, and 27.7 in gorilla. In Figure 10 this index appears, therefore, $3\frac{1}{2}$ to $5\frac{1}{2}$ times greater in man and the apes than in the macaque, i.e., this particular proportion deviates

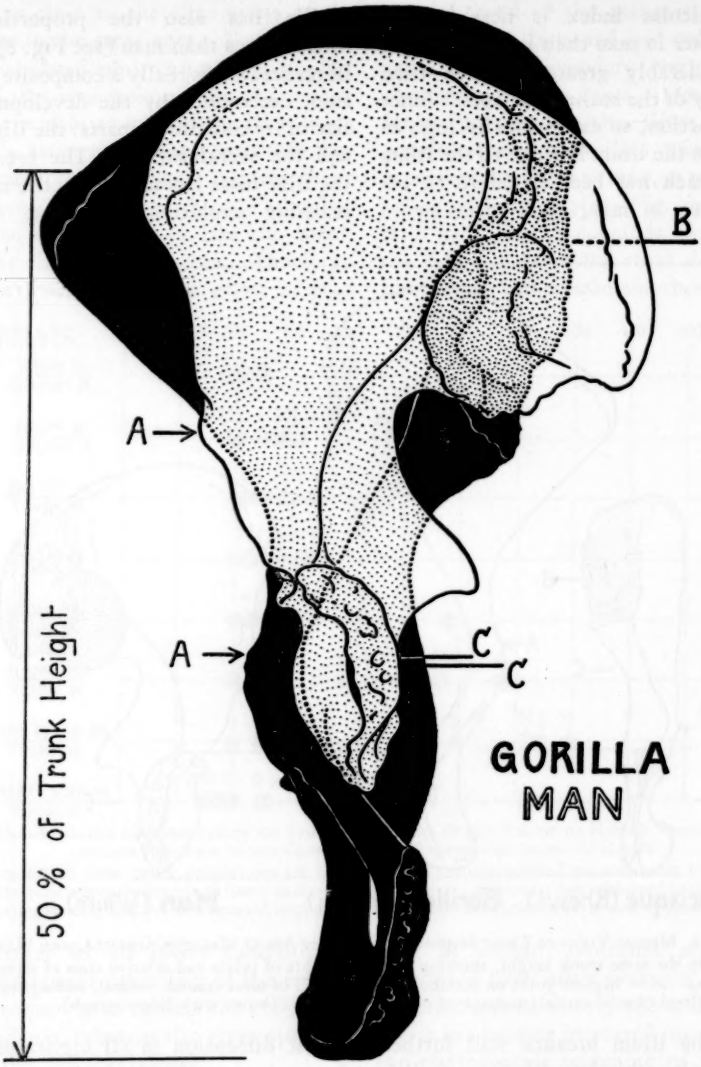

FIG. 12. MEDIAL VIEWS OF RIGHT INNOMINATE BONES OF GORILLA AND OF MAN

Reduced to the same trunk height and superimposed so that the levels of the uppermost, ventral, midsagittal points of the sacra (*B*) and the ventral borders of the sacral surfaces coincide. *A*, *B*, and *C* as in Figure 11. (Drawn with dioptrograph).

in the higher primates farther from the primitive condition than any other pelvic proportion in the diagram. It is of special interest to find that the iliac fossa portion of the ilium is proportionately narrower in man, and hence less specialized, than in

any of the great apes and that, therefore, it must be the sacral portion of the ilium which is so strongly developed in man to produce the great total breadth of the human ilium. In a former paper the author (1930a) had demonstrated that with the acquisition of the erect posture man developed an exceptionally large sacral surface at which the entire weight of the presacral portion of the body is transmitted to the lower limbs. In the brachiators (*Hylobatidae*, orang-utan and chimpanzee) the sacral surface is consistently somewhat smaller than in the quadrupedal macaque, langur and gorilla. The last proportion in Figure 10 shows clearly all these differences and particularly the exceptional position of man in regard to the relative sacral surface breadth. In the Figures 11 and 12 this enormous development of the sacral surface of the human ilium, produced by new growth in a dorsal direction, is strikingly apparent.

It can now be stated that the unique form of the human ilium is largely the result of the combination between an exceptionally low ilium height and a quite extreme breadth of the sacral surface which is unquestionably an exclusively human specialization.

There exist still other peculiarities in the human pelvis. Its position within the trunk differs fundamentally from the uniform position in the trunks of all other primates, as was shown by the writer (1930a) in a former paper and as is indicated also by the examples in Figure 13.

In the Figures 11 and 12 the levels of the end points of the midsagittal, ventral profile of the sacrum (*B* and *C*) are shown on the drawings of the innominate bones. In the macaque the caudal end of the sacrum lies high above the uppermost point of the *acetabulum* (*A*), in the gorilla at about the same level, but in man far below the *acetabulum* and, indeed, far below the *symphysion*. This very marked difference, according to which the sacrum reaches in man down to a point opposite the middle of the pubic symphysis, whereas in the gorilla merely to the level of the top of the *acetabulum* and in the macaque even only to a little below the sacral surface of the ilium, plays an important rôle during the act of birth. In macaque and gorilla, as well as in all other

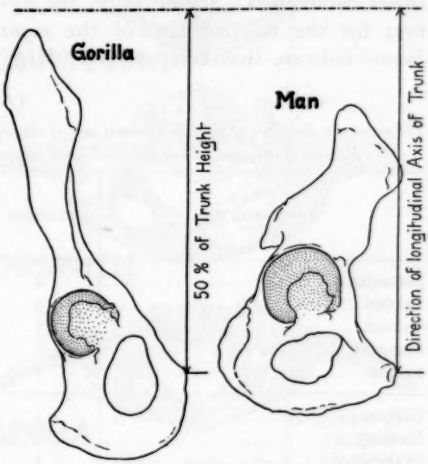

FIG. 13. LATERAL VIEWS (PERPENDICULAR TO PLAIN OF ACETABULAR RIM) OF RIGHT INNOMINATE BONE OF GORILLA AND OF MAN

Reduced to the same trunk height, showing difference in size of acetabula. (Drawn with dioptrograph.)

monkeys and apes examined for these conditions, there is no fixed, bony structure opposite the pubic bones, as exists in man in form of the lower part of the sacrum. In the former, therefore, the sacrum interferes not nearly as much with the passage of the fetus to be born, as in the latter.

As shown by Figure 13, the acetabular region of the pelvis is relatively much thicker in man than in the gorilla and the *acetabulum* itself is very much wider in

the former than in the latter. This unquestionably implies that the head of the femur is proportionately larger in bipedal man than in the largely quadrupedal apes. That this conclusion is correct is demonstrated by the data in Table 5. It is seen that man is characterized by the proportionately largest head of the femur among all the primates studied, though the great apes also possess much larger proximal joints on the femora than any of the lower catarrhines. Incidentally, the figures for the relative size of the *caput humeri* indicate that comparatively large proximal joints are characteristic for the upper as well as the lower extremity in all the higher primates. Since man manifests this general trend even in his upper limbs, it is to be assumed that the large size of his proximal femoral joints has merely become accentuated by the mechanical requirements of bipedal locomotion. The relative size of the proximal joints of the limbs is very evidently not dependent upon the relative lengths of the limbs, but is greatly influenced by body weight, considering also mode of locomotion. The last column of Table 5 reveals the fact that in all higher primates the *caput humeri* has a diameter from 13 to 25 per cent larger than the diameter of the *caput femoris*, with the one exception of man, in whom the *caput humeri* is invariably much smaller than the *caput femoris*.

After this digression one more differentiating feature of the pelves of higher primates has to be mentioned. As is strikingly evident from the dioptrographic drawings in Figure 14, the iliac fossae of man face one another, i.e., toward the midsagittal plane, whereas in all other higher primates they are pointing practically in a transverse direction. In the latter the ilia offer very little, if any, direct support for the abdominal viscera, as they do in man, and serve merely as attachment surface for muscles. The enormous development in size of the iliac fossae of the gorilla must have occurred in direct response to the specially great need for increased attachment surface for the powerful musculature of this giant ape, very much as sagittal and occipital crests develop whenever unusually large temporal and nuchal muscles require additional attachment areas.

TABLE 5

The transverse diameters of the caput femoris and of the caput humeri in percentage of the trunk height and the transverse diameter of the caput humeri in percentage of the transverse diameter of the caput femoris in adult primates

ADULT PRIMATE	SPECIMENS	CAPUT FEMORIS / TRUNK HEIGHT	CAPUT HUMERI / TRUNK HEIGHT	SPECIMENS	CAPUT HUMERI / CAPUT FEMORIS
Macaque	4	4.3	4.4	4	102.4
Baboon	3	5.4	5.4	5	103.0
Guenon	3	4.0	4.3	3	106.5
Mangabey	2	4.2	4.1	2	98.3
Langur	1	4.8	4.8	1	100.0
Gibbon	1	5.5	6.7	7	113.0
Siamang	.....	.....	.....	3	119.0
Orang-utan	1	7.6	8.8	2	117.3
Chimpanzee	4	7.5	8.6	5	118.7
Gorilla	3	8.2	10.6	9	124.9
Man	15	9.1	8.2	15	89.7

The pelvis has here been discussed in considerable detail not only because it is a complicated structure which has undergone marked changes in all higher primates, but also because the human pelvis shows many specializations peculiar to man. It is beyond any doubt that in the higher primates the ilium has become remodelled much more profoundly than the other and more uniform pelvic components and that it is chiefly in regard to the ilium that the pelvis of man is separated from the pelves of any of the anthropoid apes. The distinguishing characters of the human ilium are so numerous and in most instances so very pronounced, whereas the ilia of all the anthropoid apes show so many basic similarities, that no theory which derives man from a gorilla-chimpanzee stock can readily account for these conditions.

The following, very similar conclusion was reached by Straus (1929) from studies dealing with still other features of primate ilia: "The human ilium would seem most easily derived from some primitive member of a preanthropoid group, a form which was lacking in many of the specializations, such as reduction of the iliac tuberosity and anteacetabular spine and modification of the articular surface, exhibited by the modern great apes. I wish to emphasize here that the anthropoid-ape type of ilium is in no sense intermediate between the human and lower mammalian forms. Its peculiar specializations are quite as definite as those exhibited by man, so that it appears very unlikely that a true anthropoid-ape form of ilium could have been ancestral to the human type."

On the other hand, Reynolds (1931) in a comparative investigation on primate pelves in relation to the mechanics of erect posture regards the pelves of the great apes as transitional forms, bridging the gap between the pelves of lower primates on one side and of man on the

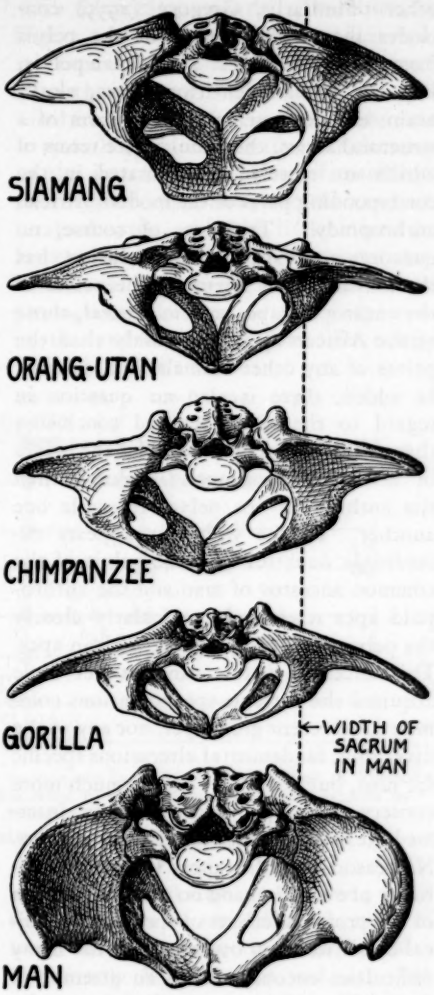

FIG. 14. CRANIAL VIEWS OF PELVES OF ADULT SIAMANG, ORANG-UTAN, CHIMPANZEE, GORILLA, AND MAN

Reduced to approximately the same greatest breadth, showing the curvature of the human ilia and the lack of such curvature in the ilia of the anthropoid apes. (Drawn with dioptrograph.) *N. B.* There exist marked asymmetries in nearly all of these pelves.

other. Similarly, Gregory (1935) concludes in a rapid survey of the pelvis from fish to man that: "The human pelvis, like the human dentition, jaws, skull, brain, etc., represents the end term of a structural series, the penultimate terms of which are closely approximated in the corresponding parts of the modern African anthropoids." There is, of course, no question in regard to the conclusion that the human pelvis resembles the pelves of the anthropoid apes and, in general, those of the African apes *more* closely than the pelves of any other animals, but, it must be added, there is also no question in regard to the more detailed conclusion that the human pelvis resembles the pelves of the African apes much *less* closely than the anthropoid ape pelves resemble one another. To the writer it appears exceedingly doubtful that the pelvis of the common ancestor of man and the anthropoid apes resembled particularly closely the pelvic type of the recent African apes. This ancestral pelvis can not yet have acquired the extreme specializations common to all recent great apes, nor any of the diverging, fundamental alterations specific for man, but must have been a much more conservative type, approximately intermediate between macaque and chimpanzee. No reasonable allowances for the reversibility of evolution and no ready admission of the profound effects of special mechanical conditions can overcome *all* the many difficulties encountered in an attempt to derive the pelvis of man from that of a chimpanzee-like ape.

Proportions of the Limbs

The main proportions of the limbs in higher primates have already been described in detail in a special paper by the author (1933b). Some of the results of this previous investigation will here be briefly reviewed with particular emphasis on the relative differences in limb proportions between lower and higher primates on one hand, and between the various types of the latter on the other hand. These proportions are illustrated by the diagrams in Figure 15.

All higher primates have in common a marked tendency to increase the length of the upper as well as of the lower extremity in proportion to the height of the trunk, but this trend is not yet nearly as evident in newborns as in adults. It is particularly noteworthy that not only man, but also the anthropoid apes, possess relatively longer lower extremities than the macaque and that not only the anthropoid apes, but also man, have proportionately longer upper extremities than the macaque and other lower catarrhines, at least at the completion of growth. In regard to the relative length of the lower limb, man represents the maximum, and in regard to the relative length of the upper limb the minimum degree of specialization among the higher primates, but nevertheless he belongs clearly in this group on the basis of both these limb proportions. The ranges of individual variations in these relative limb lengths can in rare cases overlap in man and some anthropoid apes. For instance, the relative lower limb length amounts to only 151 in an adult Hawaiian, whereas to 153 in two adult gibbons and the relative upper limb length equals 174 in an adult Negro, but only 148 and 160 in two adult mountain gorillas and 166, 168 and 173 in three adult chimpanzees (Schultz, 1933b). No adult man, however, has ever been found who possesses at the same time as long an upper *and* as short a lower limb length as any anthropoid ape.

The average relative lower limb length in adult man is slightly over 75 per cent greater than in adult macaques, but the relative upper limb length in adult gibbons

and siamangs is nearly 125 per cent greater than in adult macaques. It appears, therefore, that the phylogenetic lengthening of the lower extremities in man has not nearly reached the extreme degree of lengthening of the upper extremities in the *Hylobatidae*. In other words, the human peculiarity of long lower limbs does not represent as extreme a specialization as the enormous lengthening of the upper limbs characteristic of the gibbon family. At birth man still possesses remarkably short limbs, his relative lower limb length being surpassed by gorilla, orang-utan and, particularly, gibbon and his relative upper limb length even by macaque and langur.

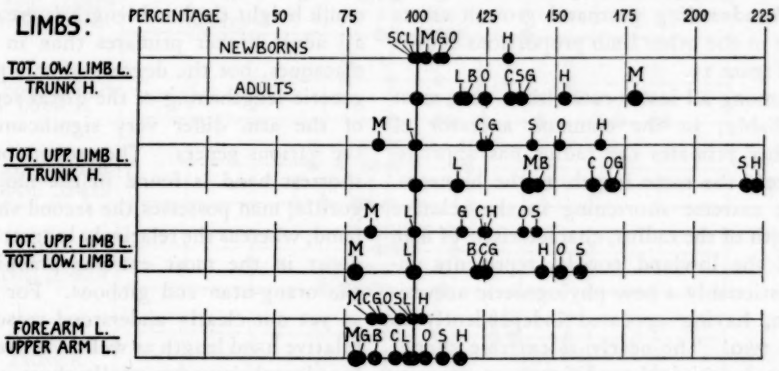

FIG. 15. DIAGRAMMATIC REPRESENTATION OF THE MOST SIGNIFICANT PROPORTIONS OF THE LIMBS IN NEWBORN AND IN ADULT HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS IN NEWBORN AND IN ADULT MACAQUE
For explanation of abbreviations see title of Figure 7

The so-called intermembral index, or the percentage relation between the total lengths of the upper and the lower extremities (third proportion in Fig. 15), is considerably more uniform than the previous two limb proportions. Among newborns as well as among adults the intermembral index is lower in man than in any of the other primates studied, but this difference becomes more pronounced with advancing growth. As shown by Figure 15, the intermembral index separates man and the anthropoid apes much more than any two of the latter are separated from one another. At the same time it must be pointed out that the decrease in the intermembral index of man from the original condition, which has been retained with probably little alteration by the macaque and other lower catarrhines, is not nearly as marked as the phylogenetic increase in this proportion in the extreme brachiators, the orang-utan, gibbon and siamang. Among adult representatives of ten different genera of lower catarrhines the intermembral index varies only between 104 and 123, but among adult higher primates this same proportion varies between 85 and 183 (Schultz, 1933b). The former, therefore, are distinguished by a remarkable constancy of the proportion between the lengths of the limbs in contrast to the latter among which this proportion shows an astonishing plasticity.

In a very similar way the brachial index, or the proportion between the lengths of

the forearm and the upper arm, ranges among lower catarrhines only between 97 and 105, whereas among higher primates between 70 and 118 (Schultz, 1933b). On an average man possesses the lowest brachial index of all simian primates at birth as well as in adult life, but in some lowland gorillas the forearm is proportionately shorter than in many Negroes. It is of great significance also that differences in this proportion between the various primates studied are not yet nearly as pronounced at birth as in adult life. The same increase in generic differences with advancing postnatal growth exists also in the other limb proportions shown in Figure 15.

Among all lower catarrhines and, most probably, in the common ancestor of higher primates the radius has approximately the same length as the humerus. The extreme shortening in the relative length of the radius, characteristic of man and the lowland gorilla, represents unquestionably a new phylogenetic acquisition, having appeared independently in the two. The nearly as extreme change from the original condition in an opposite direction, i.e., the great proportionate lengthening of the radius, most pronounced in the gibbons, must also be regarded as a new specialization.

In regard to these limb proportions adult man is least removed from the gibbon in one instance, from the mountain gorilla in two instances, and from the lowland gorilla in the remaining instance. The differences in the proportions appertaining to the upper extremity (relative length of upper limb and brachial index) are smaller between man and one or the other gorilla than between the particular gorilla and chimpanzee, but the differences in the proportions based upon the lower extremity (relative length of lower limb and intermembral index) are larger between man and the nearest anthropoid ape (gibbon and gorilla respectively) than even between gibbon and gorilla. It can be concluded, therefore, that in regard to the proportions of his upper extremity man stands very close to some anthropoid apes, whereas in the proportions of his lower extremities he has become far removed from all other higher primates.

Proportions of Hand

The differences between various primates in regard to the proportions of the hand are shown in Figure 16. In relation to the trunk height the hand length is greater in all adult higher primates than in adult macaques, but the degrees of this phylogenetic lengthening of the distal segment of the arm differ very significantly in the various genera. The proportionately shortest hand is found in the mountain gorilla; man possesses the second shortest hand, whereas the relatively longest hands occur in the most extreme brachiators, the orang-utan and gibbons. For some, as yet not clearly understood reason the relative hand length as well as the relative foot length is exceptionally short in newborn man, in contrast to the newborns of other higher primates.

If the length of the hand is expressed in percentage of the length of the proximal and middle segments of the upper extremity, it is found that chimpanzee and orang-utan have much higher indices than the siamang and gorilla, while man occupies an intermediate position in this respect. This indicates that an increase in the relative total length of the upper limb (see Fig. 15) does not necessarily affect the length of the hand to anywhere near the same degree. For instance, the total upper limb length in relation to the trunk height averages in lower catarrhines 118 and in siamangs it has increased to 233, but the hand length in relation to the

combined lengths of forearm and upper arm averages in the former 35 and in the latter only 28. Man and gorilla are distinguished by the shortest hands of all higher primates not only in relation to the trunk height but also in relation to the limb length, and in the mountain gorilla the hands are proportionately even shorter than in man. (For further details on this and the following hand proportions see Schultz, 1933b).

Among newborns man possesses the highest relative hand breadth; this is most probably due to the exceptional shortness of the hand in newborn man. The relative hand breadth decreases in general with age in man and all other primates studied (Schultz, 1926), except in the gorilla in which the hand is still comparatively slender during middle fetal life (see, e.g., Schultz, 1927, Plate V). If it is concluded from this that the extreme breadth of the gorilla hand is a late phylogenetic acquisition, as it is a late ontogenetic one, it must be assumed consistently that man developed the second broadest and shortest hand at a comparatively early stage of his evolution and has probably never possessed the typically long and slender brachiator's hand.

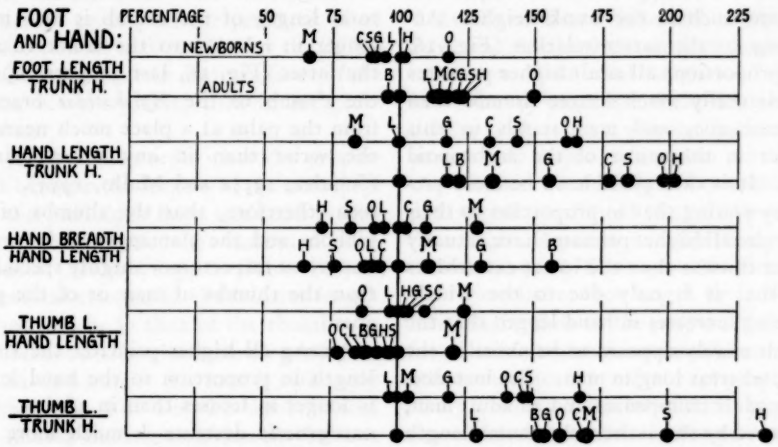

FIG. 16. DIAGRAMMATIC REPRESENTATION OF THE RELATIVE FOOT LENGTH AND SOME PROPORTIONS OF THE HAND IN NEWBORN AND IN ADULT HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS IN NEWBORN AND IN ADULT MACAQUE
For explanation of abbreviations see title of Figure 7.

The adult *Hylobatidae*, orang-utan and chimpanzee have proportionately narrower hands than the macaque, whereas man and, particularly, the two species of gorilla have developed much broader hands (Fig. 16, third proportion). As in the brachial index, so in this hand index there clearly exist divergent evolutionary trends among the higher primates. The gibbon with a relative hand breadth of only 23.8 (average of 16 adults) represents one extreme and the mountain gorilla with an average index of 58.5 the opposite extreme.

In relation to the length of the hand the total length of the thumb is greater in man than in the macaque, whereas shorter in all the anthropoid apes (Fig. 16, fourth proportion). At first glance this difference between man and the anthropoid apes

is so striking that it is sometimes asserted that the thumbs of the latter have become atrophied in consequence of their arboreal habits (e.g., Clark, 1935) or that the thumb of man has undergone a decided lengthening (e.g., Gregory, 1934). Since, however, the length of the hand in general has undergone changes with widely differing intensity, it is evident that the thumb length should be compared not only with the frequently changed hand length, but also with an independent measure, such as the trunk height. According to the latter relation (Fig. 16, fifth proportion) all adult higher primates possess really much longer thumbs than the macaque, and man stands in this respect in the midst of the anthropoid apes. It is thus possible to be more precise by stating that in proportion to their body size all higher primates have actually longer thumbs than the lower catarrhines and that it is only due to the widely differing increases in hand length that the thumb merely appears to be short in the apes, whereas long in man. For instance, in an adult chimpanzee and an adult man, measured by the author, the thumb length equals 24 per cent of the trunk height in both, but the hand length amounts to 53 per cent of the trunk height in the former and only to 36 per cent in the latter. It is to be expected, therefore, that in relation to the widely differing hand lengths the thumb length is also very different in the two, namely 46 in the chimpanzee, whereas 68 in man.

Another factor has to be considered in connection with a discussion of the length of the thumb and that is the relative length of the free portion of the thumb beyond its place of branching from the palm. Only in the *Hylobatidae* does the "free thumb" include a large part of the first metacarpal bone, whereas in some gorillas only the distal part of the basal phalanx belongs properly to the free portion of the thumb. According to Midlo (1934), who has studied this question in detail, the free length of the first digit in percentage of the palm length amounts on an average to 70 in *Hylobatidae*, to 56 in man, to 44 in the chimpanzee, to 40 in the lowland gorilla, and to 34 in the orang-utan; i.e., the part of the thumb not included in the palm is proportionately much longer in gibbons and siamangs than in man. In the former the total length of the thumb is also much longer in relation to the trunk than in the latter (Fig. 16, last proportion) and the thumb of the *Hylobatidae* branches from the palm at a place much nearer to the wrist than in any other primate (Schultz, 1933a and Midlo, 1934). It is seen, therefore, that the thumbs of the gibbons and the siamangs are in several important respects more highly specialized than the thumbs of man or of the great apes.

Among all higher primates the thumb length in proportion to the hand length is longer in fetuses than in adults. This ontogenetic decrease is much more pronounced in chimpanzees than in man and this chiefly on account of the differences in the growth changes of the relative lengths of the hands.

The rotation of the thumb, by which the first digit has come to face the lateral fingers even when adduced, is little developed in the lower catarrhines in contrast to the higher ones and is not yet present in early fetal life of any primate. Among adult higher primates this rotation, which greatly facilitates the complete opposability of the thumb, is even more advanced in some chimpanzees than in the average man (see e.g. Schultz, 1931b, Fig. 22).

In all lower catarrhines, all orang-utans, and the large majority of the African apes the second finger is significantly shorter

than the fourth. In an exceptional chimpanzee or gorilla these two fingers may be equally long. In man the second finger surpasses the fourth in length in many Whites and in small percentages of Negroes and of Indians (Steggerda and Millar, 1936). Among the *Hylobatidae* a second finger, longer than the fourth, is particularly common, having been found in 19 out of 49 gibbons and in 10 out of 14 siamangs (Schultz, 1933a). In this respect, therefore, man and the *Hylobatidae* are unique among all the primates, since in platyrrhines and prosimians the difference between the two digits in favor of the fourth is even greater than in most catarrhines.

It is also noteworthy that the proportions between the lengths of the metacarpi and the phalanges have remained practically unaltered in the various higher primates (Schultz, 1930a, Table 30) by the radical changes in the relative length of the hand or in that of the thumb. It will be shown in the following chapter that in this respect the foot is strikingly different. It will also be demonstrated that among the higher primates the foot is not nearly as conservative and comparatively uniform as the hand, but has undergone much more far reaching specializations in connection with such different modes of locomotion as exist, e.g., in orang-utan and man.

Proportions of the Outer Foot and of the Foot Skeleton

The foot in proportion to the trunk is longer in adult higher primates than in the adult macaque, with the exception of the mountain gorilla (Fig. 16, first proportion). The extreme in relative foot length has been attained by the orang-utan, and man stands in this respect between langur and chimpanzee. The exceptionally short relative foot length of the mountain gorilla is compensated for by the greatest relative foot breadth among all simian primates. The second highest relative foot breadth is found in the lowland gorilla and the third in the chimpanzee. Man ranks fourth in this proportion, i.e., the human foot (without digit I) is narrower than the foot of the African apes and is more similar in length-width proportion to the feet of lower catarrhines (Schultz, 1933b).

As stated above, man and chimpanzee have practically the same foot lengths in relation to their trunk heights. In man, however, 49 per cent of the foot length belong to the tarsus, whereas in the chimpanzee only 35 per cent, and 21 per cent of the human foot length represent the phalangeal portion of the middle toe in contrast to 36 per cent in the chimpanzee (Schultz, 1930a, Table 31). It is evident that the relative foot length by itself and comparative data on the proportions of the foot skeleton alone are insufficient for a full comprehension of the phylogenetic changes which must have taken place in the relations between the lengths of the various elements of the foot skeleton. It is necessary to correlate the size of tarsus, metatarsus and phalanges with the general size of the animal, as represented by the trunk height. These correlations are shown in Figure 17. The first proportion expresses the length of the tarsus in percentage of the trunk height. It is seen at once that man is characterized by the relatively largest tarsus, though in the gorilla the tarsus is but little smaller than the average of man and equally large as some individual human variations (see e.g. Fig. 19). The length of the metatarsal region in relation to the trunk height is larger in all higher primates than in the macaque and differs comparatively little among the former. The length of the

middle metatarsal bone is also quite uniform in its relation to the total length of catarrhines (Schultz, 1930a). That the metatarsal region is the most constant

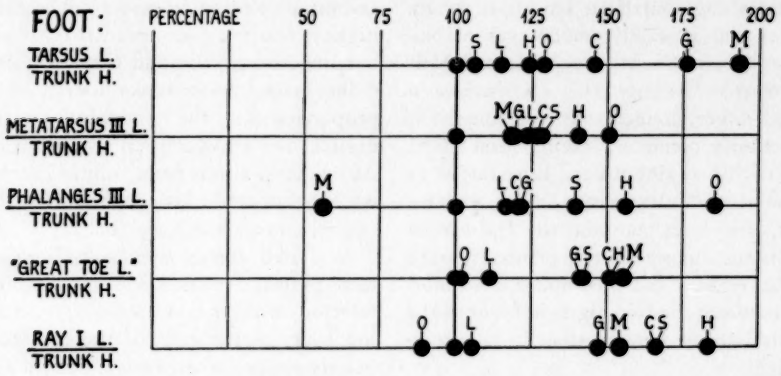

FIG. 17. DIAGRAMMATIC REPRESENTATION OF SOME PROPORTIONS OF THE OUTER FOOT AND OF THE FOOT SKELETON IN ADULT HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS IN ADULT MACAQUE

The data used for this figure are based upon as yet only partly published measurements by the author taken on the same adult specimens, as listed in the title of Figure 9. Measuring technique of foot skeleton discussed in another paper by the author (1930a). For explanation of abbreviations see title of Figure 7.

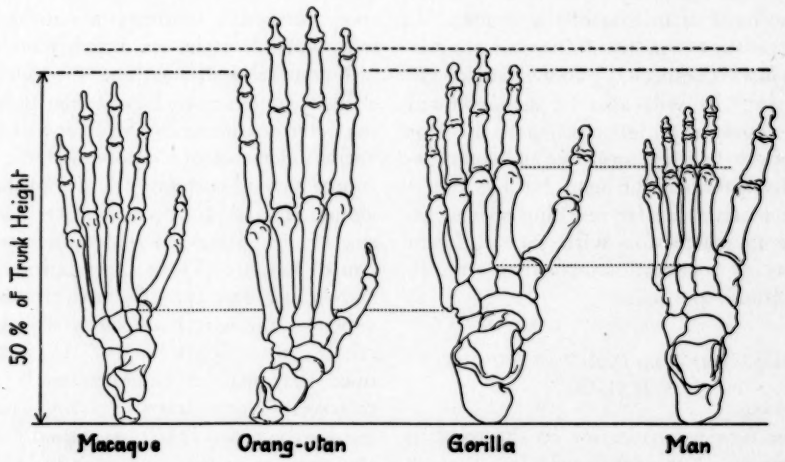

FIG. 18. FOOT SKELETONS OF ADULT MALE MACAQUE (RHESUS), ORANG-UTAN, LOWLAND GORILLA, AND MAN (HAWAIIAN)

All reduced to the same trunk height. (Drawn with dioptrograph)

the foot skeleton in man and all anthropoid apes, but this proportion is somewhat smaller in the higher than in the lower part of the foot skeleton is also readily seen by the examples in Figure 18.

The length of the third segment com-

posing the total foot length, or the phalangeal portion, differs widely among higher primates not only in relation to the length of the tarsal and metatarsal region, but also in relation to the height of the trunk (Fig. 17, third proportion). In regard to both these relative measurements man represents one extreme and the orang-utan the opposite extreme, i.e., man has by far the shortest and the orang-utan the longest phalanges not only in relation to the total foot length, but also in proportion to the size of the body; indeed, these are the most extreme specializations in phalangeal length among all the many simian primates examined by the author.

The foot skeleton of the orang-utan is characterized by one of the shortest tarsal portions among higher primates in addition to the longest phalangeal portion, whereas the corresponding human peculiarities consist in a combination of the longest tarsus and shortest phalanges. This tremendous difference is most strikingly shown by the percentage relation between the length of the phalanges (III) and that of the tarsus, which averages only 43 in man, whereas 166 in orang-utan. It is significant in this connection that this same proportion still amounts to 89 in human fetuses of the tenth week, i.e., to nearly as much as in the adult chimpanzee with an average of 101 (Schultz, 1930a, Table 32).

The unique phylogenetic shortening of the phalangeal portion of the toes in the only true bipedal primate, man, has affected most of all the middle phalanges, which form only 24 per cent of the total phalangeal length (III) in man, whereas roughly 33 per cent in orang-utan, the *Hylobatidae* and most lower catarrhines (Schultz, 1930a, Table 33; see also Fig. 18). Furthermore, only in man does one encounter the complete lack or, at least, the fusion with the distal phalanx of the middle phalanx of, particularly, the fifth toe, a condition already occurring in a majority of the cases in some human races.

In man alone does the great toe reach as far as, or even farther than, any of the other toes, at least during postnatal life. From this many authors have concluded even in recent times that the great toe of man has become longer, or has hypertrophied in general (e.g. Clark, 1935 and Gieseler, 1936). However, Schwalbe (1916), Virchow (1917), Weidenreich (1921) and the author (1930a) have already pointed out that it is not the great toe of man which has become longer, but the lateral toes II to V which have become shorter. If the great toe length (from heel to tip of great toe) is expressed in percentage of the trunk height (Fig. 17, fourth proportion), man stands most removed from the macaque, but gibbon and chimpanzee are very close to man in this respect. The "great toe length," as used on the outer foot, is composed in the skeleton of the tarsal length in addition to the length of the first digital ray. The latter length by itself equals exactly 100 per cent of the former length in man, whereas 122 per cent in chimpanzee (Schultz, 1930a, Table 32). If, therefore, the length of only ray I is expressed in relation to the trunk height (Fig. 17, last proportion), it is found that, considering the size of the animal, gibbon, siamang and chimpanzee possess actually longer great toes (phalanges + metatarsus I) than does man. That the human hallux is but very little longer than the hallux of the gorilla, when both have been reduced to comparable size of the trunk, is clearly shown by Figure 19. The same figure, as well as a comparison between the various foot proportions in Figure 17, demonstrates beyond any doubt that the most striking morphological distinction between the foot skeletons of man and

gorilla consist in the different relative lengths of the phalanges of the lateral toes. The human specialization in this respect does not diverge any more in one direction than do the peculiarities of the orang-utan foot in the opposite direction.

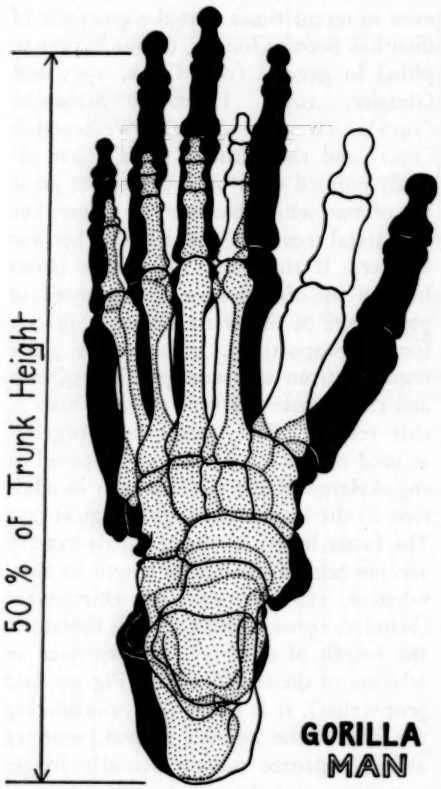

FIG. 19. FOOT SKELETONS OF THE ADULT GORILLA AND MAN, shown in Figure 18, SUPERIMPOSED
Reduced to same trunk height. (Drawn with dioptrograph.)

The latter are most evident in the great length of the phalangeal portion of the lateral toes and in the striking reduction, amounting to a degeneration, of the hallux (see Fig. 18). In many orang-utans the terminal phalanx and the nail of the great toe is missing, just as in man the middle phalanx of the reduced fifth toe is frequently absent and the nail rudimentary or also lacking. These marked reductions of the great toe in orang-utan are already present in fetal life and are hence not due to self-mutilation, as suggested by Yerkes and Yerkes (1929, p. 107). The degenerate great toe of orang-utan has lost the faculty of complete adduction in many old individuals, but can be abduced much farther than in the gorilla. The great toe of man with its opposite specializations has lost the power of, at least metatarsal, abduction, though the joint at its base still shows unmistakable traces of former movability (Schultz, 1930a, Fig. 22).

The proportions and the skeletal parts of the foot of man can readily be explained as modifications of a generalized and conservative anthropoid ape type of foot. A very similar conclusion has been reached in regard to the mechanical construction of the foot by Morton (1927) and by Elftman and Manter (1935). Many fetal growth changes in the human foot also support this view (Schultz, 1926). It must be emphasized, however, that in all these conditions the differences between the foot of man and the generally most similar foot, that of the gorilla, are far greater than the differences between the feet of gorilla and chimpanzee.

In regard to the foot musculature the gap between man and the anthropoid apes is apparently considerably greater than that existing in regard to the skeleton and the proportions. Thus, Wells (1931) concludes: "The fact that the soft anatomy of the human, and especially of the Bantu foot, is less differentiated from a generalized type than that of the foot of the anthropoid apes, so as to present a surprising resemblance to that of the baboon's foot, indicates that the separation of the

human from the simian stem took place when both were but little differentiated from the ancestral catarrhine stock, from which the Cercopithecidae also arose." Based upon his extensive studies on the foot musculature in primates, published in 1930, and upon many later, additional observations Dr. W. L. Straus, Jr. has reached essentially the following conclusions, which he has kindly permitted to be mentioned here: If the foot musculature as a whole is considered, the gorilla resembles man more closely than does any other primate. In certain important muscular details, however, the human foot is much more primitive and generalized than are the feet of gorilla and other anthropoid apes and approaches the conditions in lower catarrhines. The foot musculature of man is most easily derived from a type which in its general plan differed but little from that found in the lower catarrhines. From this ancestral type the resemblances between man and the anthropoid apes resulted by parallel and independent trends.

Proportions of the Head

The relative differences between the various primates studied in regard to some of the proportions of the head are illustrated in Figure 20. All the higher primates possess relatively larger heads than the macaque and this already at birth. Among the new-borns orang-utan and gibbon have the proportionately larger heads than man (see chapter on relative cranial capacity, notes on newborns), but during postnatal life the head of man continues to increase in size more intensively and for a longer period than in the anthropoid apes, so that man acquires the relatively largest head among adults.

The relation between the total face height and the trunk height removes man from the large apes, inasmuch as all the latter have proportionately much larger faces than the former. At birth the *Hylobatidae* possess in relation to the size of their trunks a higher face than man, but in adults this proportion has become somewhat greater in man than in gibbons and siamangs on account of a less pronounced postnatal growth change in the former than in the latter.

In proportion to the size of the brain part of the head the face part is smaller in man than in any of the other primates studied (Fig. 20, third proportion), a difference even more marked at birth than at the completion of growth. The unique position of man in regard to this particular index is to be expected, since it is man among all higher primates in whom the largest brain part is combined with one of the smallest face parts of the head.

Man possesses at all ages a comparatively broad interocular region, indeed, among adults he surpasses in this respect all other higher primates (Fig. 20, fourth proportion). The gibbon approaches man most closely in regard to this relative distance between the eyes. It may be mentioned here that, according to comparative anatomical and growth studies, a broad interocular region must be regarded as a primitive character. Hence the orang-utan with its extremely narrow width between the eyes is more highly specialized than man with his broad width, though the latter is more advantageous for stereoscopic vision.

The relative size of the outer ear (ear height × ear breadth in percentage of head length × total head height; Fig. 20, fifth proportion) varies very extensively among higher primates, namely between only 2.5 in some adult orang-utans and 20.3 in some adult chimpanzees. In the latter the ears have become greatly overdeveloped, whereas in the former they have degenerated to the smallest relative

size among all primates. The same proportion varies among adult lower catarrhines only between about 9 and 19. The relative ear size furnishes one more of the many examples in support of the general claim that, in comparison with the numerous and uniform lower catarrhines, the few types of higher primates are characterized by a conspicuous facility indicated, little more of the helix being bent over than in the lower catarrhines (Schultz, 1931b and 1933a). A true and large ear lobule, free of cartilage, is found only in the majority of human beings and in some chimpanzees and gorillas.

Among the adult higher primates man stands nearest to the gorilla in regard to relative head size and relative ear size,

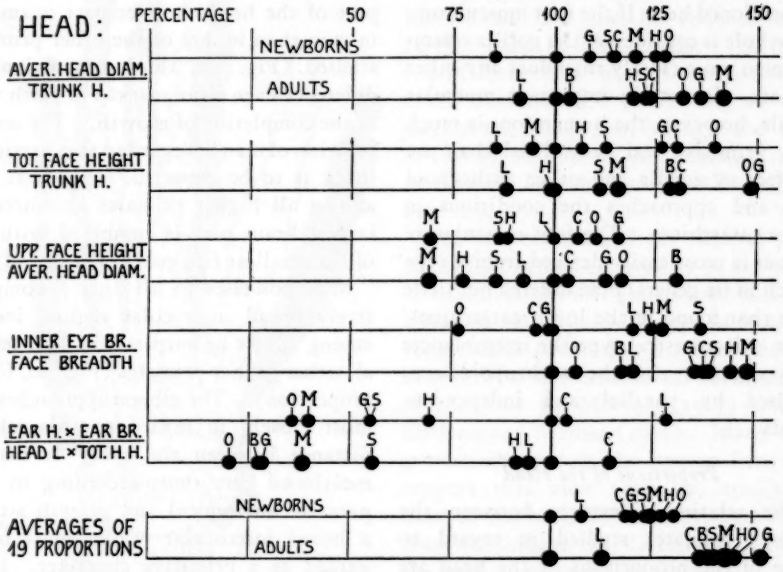

FIG. 20. DIAGRAMMATIC REPRESENTATION OF THE MOST SIGNIFICANT PROPORTIONS OF THE HEAD AND AVERAGES OF ALL THE BODY PROPORTIONS (in the Figures 8, 15, 16, and 20) IN NEWBORN AND IN ADULT HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS AND AVERAGES IN NEWBORN AND IN ADULT MACAQUE

For explanation of abbreviations see title of Figure 7

for far reaching and widely divergent specializations.

The higher primates have in common a marked tendency for the free edge of the ear (*helix*) to become rolled in during postnatal growth. This is decidedly most pronounced in gibbons and siamangs and is also very evident in orang-utans, gorillas and most human races. In chimpanzees, however, this trend is usually only nearest to the gibbon in regard to relative upper face height and relative interocular width, and nearest to the siamang in regard to relative total face height.

Average Generic Differences in Regard to Proportions of Outer Body

Some strictly limited, yet very significant and condensed information can be gained from a study of the *average* relative

differences between the higher and lower catarrhines in regard to all the proportions, appertaining to the outer body, discussed in this paper (see Fig. 20, bottom). These averages disregard quite properly whether a particular deviation from the condition in the macaque falls on the right or on the left of the line representing the macaque; in other words, the absolute differences between corresponding proportions in higher primates and macaque (and not the absolute values in the former) are expressed in percentage of the values in the latter regardless of *plus* or *minus* sign, since these *averages* are intended to show merely the relative amounts of the general differences, but naturally not the direction of these differences.

Among adults the particular body proportions considered here differ on a general average from the same proportions in the macaque by the following percentages of the values in the macaque: Langur = 12.7; chimpanzee = 37.2; mountain gorilla = 39.2; siamang = 40.8; man = 43.4; gibbon = 43.9; orang-utan = 45.7; lowland gorilla = 52.0. These figures demonstrate first of all that *all* higher primates differ much more from the macaque than the latter representative of the subfamily *Cercopithecinae* differs from the langur, representing the subfamily *Semnopithecinae*. In regard to the general average of his body proportions man stands in the midst of the anthropoid apes and this among adults as well as among newborns. Several of the apes have in general deviated farther from the conditions in the lower catarrhines than has man. As shown by a glance at Figure 20, all higher primates and the langur stand in regard to the aggregate condition of their body proportions much closer to the macaque at birth than at the completion of growth. This result could not be expected without the conclusion that all higher primates developed from some common ancestor which closely resembled the conservative forms among the recent lower catarrhines and from which the latter as well as the former inherited the same plan of growth which later became altered here or there by gradually increasing ontogenetic modifications producing the diverging, phylogenetic specializations.

SUMMARY AND CONCLUSIONS

Most of the specific and detailed data collected and discussed in this paper are enumerated in a very condensed manner in Table 6, which serves as a convenient summary and as a general basis for the following conclusions.

The group of higher primates is characterized first of all by its striking plasticity as manifested by its enormous generic variability in contrast to the comparative uniformity among the lower catarrhines. This difference becomes particularly impressive when it is recalled that (chiefly according to Elliot, 1913) the family *Cercopithecidae* consists of 16 recent genera and approximately 260 species, whereas the higher primates are composed of only 6 recent genera containing at most 28 species. It is with the few higher primates that evolution has made the most far reaching experiments, carrying them not only to widely differing levels along the same directions, but also in many respects in greatly diverging directions. The multitudinous Old World monkeys, on the other hand, represent as a whole a remarkably homogeneous and fairly primitive group regarding their fundamental anatomical characters, when compared with the remaining catarrhines, the anthropoid apes and man. That the *Cercopithecidae* have in general been content with minor specializations and that the higher primates alone have possessed the

TABLE 6

Summarizing list of comparisons between the various higher primates and the macaque in regard to sixty characters discussed in this paper

Nearly all the figures are approximate averages, omitting the decimals. * = highest degree of specialization; ** = highest degrees of divergent specializations.

CHARACTER	LOWER CATARRHINES e.g. *Macaque*	HYLOBATIDAE		ORANG-UTAN	CHIMPANZEE	GORILLAS		MAN
		Gibbon	Siamang			Lowland	Highland	
Duration of Pregnancy (Conception age in days)	166	209	?	275*	235	?		266*
Duration of postnatal Growth (Completion of permanent dentition in years)	6.8	?	?	?	10.9	?		19.9*
Approximate Weight of Newborn (in g.)	435	360	?	1500	1600	1800	?	3200*
Approximate Weight of Adult Male (kg.)	9	6	11	72	60	200*		75
Ratio between cranial Capacity and Body Weight in Adults	1:94 (♂) 1:70 (♀)	1:61 (average)	1:86 (average)	1:139 (♂) 1:171 (♂)	1:149 (average of ♂)		1:157 (♀)	1:40 to 60*
Chief Mode of Locomotion	quadrupedal	bimanual** more bipedal than great apes		bimanual**	quadrupedal and bimanual	quadrupedal and bimanual		bipedal**
Position of Fingers in quadrupedal Locomotion	straight or extended	straight		flexed*	flexed*	flexed*		straight
Number of Hairs per sq. cm. of Skin in Adults (Schultz, 1931): Scalp	910	2035**	718	158	112**		440	312
Back	866	1727**	429	176	48		127	0**
Chest	172	499**	251	107	21		5	1**
Ischial Callosities	always present, ontogenetically early	always present, small, ontogenetically late		very rare and not really horny	present in 38 per cent of cases	very rare and only little developed when present		never present*
Changing sexual Skin of Females	present	absent(*?)		absent(*?)	present	present		absent(*?)
Average menstrual Cycle (in days)	28	?		32	ca. 35(*?)	?		28
Penis Bone	present	present		present	present	present		absent*

Frontal Sinuses	absent	absent		small sinuses present in some cases	generally large, occasionally *very* small	always very large*	small to large, occasionally lacking
Os centrale of Wrist fuses with Os naviculare	never	frequently in old age		occasionally in old age	in late fetal or even infantile life	in an infant of 3.5 years not yet fused	during 3rd fetal month*
Nasal Bones fuse in	fetal life	juvenile life (after eruption of M1)		juvenile life	juvenile life, rarely in sub-adults	juvenile life, sometimes in sub-adults	only in old age in very rare cases*
Average Total Number of Vertebrae	48.9	32.1	31.6	30.8*	32.6	32.3	33.4
Average Number of Thoracolumbar Vertebrae	18.9	17.9	17.4	16.0*	16.8	16.6	17.0
Average Number of Sacral Vertebrae	3.0	4.4	4.5	5.1	5.4	5.6*	5.2
Average Number of Coccygeal Vertebrae	ca. 17.0	2.7	2.6*	2.8	3.2	3.0	4.2
Length of Cervical Region of Spine in % of Trunk Height	18	17		24	23	24	26*
Length of Lumbar Region of Spine in % of Trunk Height	45	25		24	17*	28	37
Proportionate Distance between last Ribs and Iliac Crests of Pelvis	very long	medium		very short	very short	extremely short*	medium
Chest Girth in % of Trunk Height	103	149	174	185	176	223*	207	162
Shoulder Breadth in % of Trunk Height	35	53	52	59	57	72*	65	67
Hip Breadth in % of Trunk Height	33	43	47	50	55	67*	58	58
Chest Breadth in % of Chest Depth	87	118	125	126	129	135	146*	129
Height of Shoulder (above suprasternal notch) in % of Trunk Height	5	12	14	16	17**	13	12	2**
Height of Nipples (above Symphysion) in % of Trunk Height	80	84	81	90**	86	82		76**
Width between Nipples in % of Chest Breadth	40	32	28**	89**	52	46		71
Total lower Limb Length in % of Trunk Height	96	147	131	119	128	131	112	171*
Total upper Limb Length in % of Trunk Height	107	238*	233	182	175	184	154	150
Total upper Limb Length in % of Total lower Limb Length	111	162	178**	170	137	140	137	88**

TABLE 6—*Concluded*

CHARACTER	LOWER CATARRHINES e.g. *Macaque*	HYLOBATIDAE		ORANG-UTAN	CHIMPANZEE	GORILLAS		MAN
		Gibbon	Siamang			Lowland	Highland	
Diameter of Caput humeri in % of Diam. of Caput femoris	102	113	119	117	119	125**		90**
Forearm Length in % of Upper arm Length	97	113**	107	101	90	78	83	77**
Hand Length in % of Trunk Height	28	56*	51	55	49	43	34	37
Hand Breadth in % of Hand Length	37	24**	29	33	35	49	58**	41
Thumb Length in % of Trunk Height	14	34*	29	23	24	22	22	24
Thumb Length in % of Hand Length	56	54	55	44**	47	52	50	68**
Free Length of Thumb in % of Palm Length (Midlo)	30	71*	68	34	44	40	35	56
Relative Position of Place of branching of Thumb from Palm (Midlo)	66	30*	40	45	44	59		55
Foot Length in % of Trunk Height	43	53	52	64*	50	52	41	49
Great Toe Length (from heel) in % of Trunk Height	31	47	44	31	46	44		48*
Length of Phalanges + Metatarsus I in % of Trunk Height	15	27**	24	13**	24	22		23
Length of Phalanges of Toe III in % of Trunk Height	15	23	20	27**	18	18		8**
Tarsus Length in % of Trunk Height	12	15	13	16	18	21		23*
Average Head Diameter in % of Trunk Height	21	26	26	28	26	29	22	30*
Total Face Height in % of Trunk Height	21	21	23	31*	27	31*	27	24
Upper Face Height in % of Average Head Diameter	73	56	62	85	75	82	95**	50**
Inner Eye Breadth in % of Face Breadth	17	25	24	18*	23	23	20	25
Relative Ear Size	14	13	8	3**	16**	4	4	5
Breadth of Manubrium sterni in % of Trunk Height	6	11	10	12	11	15*		12
Breadth of Corpus sterni in % of Length of Corpus sterni	13	39	53	58*	21	45		38
Ilium Height in % of Trunk Height	25	32	35	36	39	40*		25
Ilium Breadth in % of Ilium Height	42	46	60	72	60	90		122*
Ilium Breadth in % of Trunk Height	11	15	21	26	23	36*		30
Iliac Fossa Breadth in % of Trunk Height	5	11	15	20	19	28*		18
Sacral Surface Breadth in % of Trunk Height	6	5	6	6	6	8		12*
Fossa Iliaca facing	ventrally	ventrally	ventrally	ventrally	ventrally	ventrally		sagittally*

* = highest degree of specialization; ** = highest degree of divergent specializations.

capacity for many radically new developments can here be illustrated by merely a few random examples. In spite of the fact that the *Cercopithecidae* include ten times more species than the higher primates, the number of true sacral vertebrae is practically always the same among the former (i.e., 3; 2 or 4 vertebrae occurring in only very rare instances), but among the latter this number fluctuates widely between 3 and 7. The relation in length between the upper and lower limbs (intermembral index) varies among adult Old World monkeys only between 104 and 123, whereas among the higher primates between 85 and 183. In all lower catarrhines the permanent canine teeth are large in males and small in females. Only among the higher primates have changes in this sex difference occurred and this even in opposite directions, namely in the gibbons and siamangs in which the canines are very large in both sexes, and in man in whom the canines are small in females and in males. Large throat pouches are unknown among all lower catarrhines, but are developed to an enormous size in siamangs and orang-utans. The body weight of normal adults ranges among the catarrhine monkeys from about 2 kg. in a talapoin to hardly more than 35 kg. in some male baboons, but among the higher primates it varies between 4 kg. in some gibbons and over 250 kg. in male gorillas. There exist far greater differences in the shape of the foot between man and orang-utan or in the size of the outer ear between chimpanzee and orang-utan than have been found in these characters among all the lower catarrhines. Among the latter the mode of locomotion is always chiefly quadrupedal, whether on the ground or in the trees, and exclusive brachiation is rarely and quite temporarily resorted to. In the higher primates alone have new modes of locomotion developed, namely the erect bipedal walk of man, the rather clumsy bipedal trot of gibbons, the extreme and highly perfected brachiation of the slow orang-utans and the rapid *Hylobatidae*, and the quadrupedal walk on the horny knuckles of the flexed fingers of the African apes.

On account of this first, and perhaps most important, common character of higher primates—their great plasticity or faculty for modifications—this group contains many divergent specializations. In spite of the latter the higher primates can properly be regarded as one natural group, because not only are they all separated from the lower catarrhines, but they also all share a great many evolutionary trends, as is manifested by those countless phylogenetic alterations which are identically directed in all, differing only in the degrees of perfection attained by the various types. Of the sixty characters listed in Table 6, sixteen have developed in divergent directions among the higher primates, but the remaining great majority contains many conditions which reveal definite single trends in all anthropoid apes and man. Of such common trends the following may be specially mentioned as outstanding examples (see also Table 6). Contrasted with lower catarrhines all higher primates have in common: Prolongations of the duration of pregnancy and the total period of postnatal growth (as far as known); the gradual disappearance of ischial callosities; a widely varying tendency for fusion of the *os centrale* with the *naviculare*; a tendency for late fusion between the nasal bones; reductions in the total number of vertebrae and in the numbers of thoracolumbar and caudal vertebrae; increases in the number of sacral vertebrae; increases in the relative length of the neck; decreases in the relative length of the lumbar portion of the spine and approximations between thorax and

pelvis; greatly increased stoutness of the trunk in general; marked increases in the widths of the shoulders, chest and hips, extensive lengthening of the lower and, particularly, the upper limb; lengthening of hand and thumb in relation to general body size; increases in relative size of head and in volume of brain (considering general body size); an enormous widening of the sternum; very large increases in the breadth of the ilium, particularly the iliac fossa; and lengthening of the tarsus. This list of phylogenetic trends common to all higher primates could easily be prolonged enormously by enumerating the findings of other investigators in the many special fields of science not even mentioned in this paper. The above random examples suffice to support the general deduction that the group of higher primates could not be characterized by manifestations of so many identical trends, if they had not been endowed with these same tendencies from one common ancestral source. Unquestionably, some of the above named and many additional common trends of higher primates are directly or indirectly connected with the gradual acquisition of the semierect and erect posture, as has been demonstrated by many authors (e.g., Knauer, 1916; Ruge, 1918; Keith, 1923; Morton, 1926; and Gregory, 1928), who have also shown that with the perfection of erect posture such trends have become most pronounced in man, producing many of the extreme conditions which appear as human peculiarities (e.g., Böker, 1935). It is very significant, however, that there also exist a great many common trends among higher primates for which neither the direction of the body axis nor the habit of brachiation can be held responsible. Thus, neither of these factors can by any reasonable argument be connected with the prolongation of the periods of growth or the comparative increase in the size of the brain, those highly important acquisitions of all higher primates. It also appears most probable that the remarkable plasticity of higher primates was a cause, rather than a consequence, of the development of the upright position.

It remains to consider the much contested problem of the phylogenetic relationships between the various higher primates and, especially, of the relation between man and the anthropoid apes.

Huxley (1864) had already dealt with this problem, reaching the classic conclusion: "that the structural differences which separate Man from the Gorilla and the Chimpanzee are not so great as those which separate the Gorilla from the lower apes" (= lower primates). He specifically added that the differences between man and even the highest apes "are great and significant" and that "the structural differences between Man and the Man-like apes certainly justify our regarding him as constituting a family apart from them." Weinert (1932), on the other hand, places man and the three great apes in one single family containing three genera: one for the orang-utan, one for both African apes, and one for man, the latter two genera representing the single group "*Summoprimates*." The evidence collected in this paper forces the author to agree essentially with Huxley and to disagree radically with the genetic implication of Weinert's classification (most clearly shown in his diagram of the primate family tree) that man and the chimpanzee are much more closely related than the chimpanzee and the orang-utan. That the latter conclusion is untenable has most recently also been shown by Straus (1936), who concludes from his comprehensive survey of the thoracic and abdominal viscera of primates that: "Each of the four apes and man exhibits a definite mosaic of visceral characters, some rather primitive, some

intermediate, and some highly specialized. There is nothing in this survey to indicate that man possesses any peculiarly close affinities with the chimpanzee, . . . or even with the chimpanzee-gorilla stock. . . . It might be claimed quite as logically, that man is most closely related to the gibbons."

According to Table 7 man resembles most closely one or the other species of gorillas in 23 out of 57 characters considered, in 15 other characters he is most similar to gibbons or siamangs, and in only the remaining 19 characters does man be arranged according to their general resemblanee, namely: man—gorillas—chimpanzee——orang-utan——*Hylobatidae*. They indicate also that the two African apes stand particularly close together. The latter conclusion is already so well established that it requires no further discussion; indeed, some writings of the past would rather make it appear necessary to emphasize that the differences between chimpanzee and gorilla are sufficiently large to justify their generic separation. It certainly is not to be doubted any more that the gorillas and chimpanzees became

TABLE 7

Numbers of characters of closest resemblance among higher primates

NUMBER OF CHARACTERS regarding which	MAN	GORILLAS	CHIMPANZEE	ORANG-UTAN	HYLOBATIDAE
Man resembles most closely	(57)	23	12	7	15
Gorillas resemble most closely	13	(57)	30	12	2
Chimpanzee resembles most closely	4	28	(57)	15	10
Orang-utan resembles most closely	5	16	19	(57)	17
Hylobatidae resemble most closely	11	8	15	23	(57)
Number of Characters showing *highest degrees of specialization* (Total = 82)	27	17	6	16	16

The numbers of the characters listed in Table 6 in regard to which any particular type of higher primate resembles most closely the other higher primates and the numbers of characters showing the highest degrees of specialization (including divergent ones) in the various types. Since some characters differ but little in the various types these figures can indicate merely the approximate, average conditions.

resemble most closely either the chimpanzee or the orang-utan. The gorillas differ least from the chimpanzee in regard to 30 of these characters and least from the orang-utan in regard to 12 other characters. According to still other data in the same table the chimpanzee approaches most frequently the gorillas and next frequently the orang-utan, and the latter stands closest to the chimpanzee and about equally close to the *Hylobatidae* and the gorillas. The gibbons and siamangs, finally, are least different from the orang-utan. These figures show chiefly the order in which the higher primates must phylogenetically divided *after* an independent branch for the orang-utan had appeared. That even the orang-utan diverged from an ancestral stock, common to the great apes, *after* the separation of an evolutionary branch for man, is the only admissible conclusion from the result, to be discussed below, that the general, average differences between the three great apes are smaller and less significant than those between any of the latter and man.

The following characters are peculiar to man and differ at least in the degree of specialization from all the great apes: in all probability the greatest increase in

the duration of postnatal growth; the greatest weight at birth in relation to body weight in adult life; the largest relative brain size; complete bipedal walk and erect posture; greatest reduction in density of hair (except on scalp) and occurrence of wavy and curly hair; universal absence of ischial callosities; probably earliest disappearance of an independent *os centrale;* rarity and lateness of fusion of nasal bones; by far the earliest obliteration of the facial sutures between maxillary and premaxillary bones; by far the latest closure of the great fontanelle; complete lack of penis bone; presence of *ossicula mentalia*, of a true inguinal ligament, and of a transverse metatarsal ligament between toes I and II; unique structure of kidney; highest total number of vertebrae; highest average numbers of thoracolumbar and coccygeal vertebrae; longest cervical and lumbar regions of the spine; the least approximation between thorax and pelvis; least increase in average stoutness of trunk; by far the lowest shoulders; lowest placed nipples; greatest average relative length of lower limbs and shortest average relative length of upper limbs; by far the lowest intermembral index; by far the longest thumb in proportion to the length of the hand and the relatively longest free portion of the thumb; straightness of fingers with extension of palm; by far the shortest relative length of the phalangeal portions of the toes II to V; complete and permanent adduction of hallux; the shortest height of the face in relation to trunk height and, particularly, to size of brain part of head; by far the shortest height of the pelvis, particularly the ilium, in relation to the trunk height and the ilium breadth; the great enlargement of the sacral surface of the ilium; the unique position of the pelvis in regard to the longitudinal axis of the trunk; the unique direction of the *fossa iliaca*; the equality of the sexes in regard to the size of the canine teeth. This, of course, is a very incomplete list, but it is sufficiently large to support the general claim that a majority of characters separate man more from the great apes than the latter are separated from one another. This general rule is not invalidated by its exceptions, since such exceptions are to be expected with the assumption of a common ancestry for man and all great apes from which they received the same initial characters, among which some can have become modified with exceptional intensity in only one or another type. Genetic relationships can never be reconstructed on the basis of isolated characters alone, but must rest upon the consideration of the more numerous and the more diverse characters the better. The facts that man and the African apes are closely alike in regard to their frontal sinuses (Weinert), their facial muscles (Huber, 1931), etc. are readily explained as instances of parallelism which, according to Clark (1936), are more common in primates than is usually assumed, and they are more than counterbalanced for phylogenetic deductions by the findings that man stands apart from all great apes, while the latter are in most instances closely alike, in regard to the long list of characters already given and in regard to a great many additional features appertaining to the fields of morphology, physiology and psychology. It must also be emphasized here that it is above all the unique combination between many primitive and many other, highly specialized characters which distinguishes man from the great apes. In the latter the typical combinations of the generic variations in the different features are much more similar and uniform than in Weinert's "*Summoprimates*"—man, chimpanzee and gorilla.

Among the characters listed in Table 6 there are 27 in regard to which man is

either most highly specialized or else represents the extreme of a divergent evolutionary trend. The corresponding figures for the anthropoid apes are much smaller, being least of all in the chimpanzee (see Table 7). The latter figures total 55. It can be stated, therefore, that in the characters discussed here man is twice as frequently less specialized than one or another anthropoid ape, as he is more specialized, yet he possesses many more extreme specializations than any one of the apes.

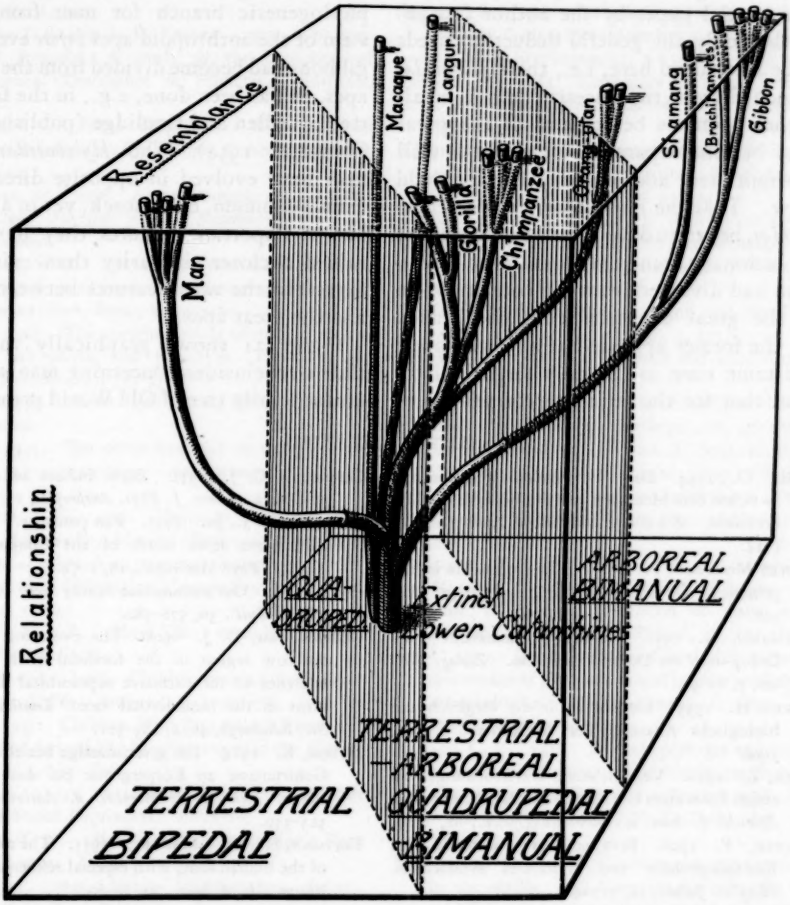

FIG. 21. HYPOTHETICAL, THREE-DIMENSIONAL PEDIGREE OF THE RECENT CATARRHINE PRIMATES AS SUPPORTED BY THE RESULTS OF THIS PAPER AND BY FORMER STUDIES OF THE AUTHOR

The macaque represents the subfamily *Cercopithecinae* and the langur the subfamily *Semnopithecinae*. The different habitats and modes of locomotion (underlined) are inscribed on the bottom square.

The many and profound similarities be-

tween the *Hylobatidae* and the other higher primates, especially the great apes, as well as the numerous peculiarities of gibbons and siamangs have already been discussed in a special paper by the author (1933a) so that only the general deduction needs to be mentioned here, i.e., the *Hylobatidae* branched from the ancestral stock of all higher primates before any of the great apes became separated. This is a well substantiated and quite generally held view. That the *Hominidae*, like the *Hylobatidae*, began to develop as an independent evolutionary branch *before* even the orang-utan had diverged from the common stem of the great apes and that the branch for the former appeared at approximately the same time as, or only slightly later than that for the latter, represents in the writer's opinion the only theory which can readily account for all the facts known today. From the available evidence it does not seem necessary to separate the phylogenetic branch for man from the stem of the anthropoid apes *before* even the gibbons had become divided from the great apes, as has been done, e.g., in the family tree by Allen and Coolidge (published by Coolidge, 1934). The *Hylobatidae* and man have evolved in opposite directions from a common, early stock, yet in a number of important features they have retained a closer similarity than exists in regard to the same features between man and the great apes.

Figure 21 shows graphically the author's conclusions concerning man's place on the family tree of Old World primates.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

THE VARIATION OF ANIMALS IN NATURE. *By G. C. Robson and O. W. Richards. Longmans, Green and Co., New York.* $8.25. $8\frac{3}{4}$ x $5\frac{3}{4}$; xvi + 425 + 1 plate; 1936.

In many ways this is an important book. It deals with an interesting subject; evaluates a large group of data critically; points out many gaps and problems yet to be attacked, and generally attests the fact that the authors have more than a reading acquaintance with much of their text discussion. The question of variation of animals in nature is a problem too often overlooked and too often underestimated. The central theme of this book has been to collect facts as to how animals vary and then apply specific evolutionary theories to these facts in an attempt to see which theory or theories best fit the actual material. This is a sound procedure.

The volume is divided into eight chapters headed as follows: Introduction, The origin of variation, The categories of variant individuals, The distribution of variants in nature, Isolation, Correlation (*i.e.*, the hanging together of blocks of characters in evolution), Natural selection, Other theories of evolution, Adaptation, and Conclusions. In the final chapter the authors set forth, in a critical fashion, their deductions about the dynamics of evolution. It is impossible to summarize many of these in so brief a review. Of particular interest, however, is the following passage about natural selection: (p. 373).

> We may, perhaps, claim to have shown that group formation is, in part at least, independent of Natural Selection; that the effect of the environment alone cannot give rise to adaptations; and that Natural Selection cannot be excluded from the possible causes of adaptations, though it is more likely to have produced specialization than the more fundamental processes of organization.

This book, distinctly modern in its ideas and approach, should be read by all biologists interested in the theoretical aspects of their subject. It blends competently the talents of the field naturalist, the experimentalist, the geneticist and the statistician. The volume has a carefully selected bibliography and a good index.

REASON AND REVELATION. *Argument for the Truth of Revealed Religion Based Solely upon the Evidences of Science and Philosophy. By Edward McCrady. Wm. B. Eerdmans Publishing Co., Grand Rapids.* $3.00. 9 x 6; 411; 1936.

With reference to evolution the author holds to the following:

> Either Evolution is development by means of energies exclusively immanent in the developing material —*i.e.*, exclusively inherent in the very constitution of *matter* itself, or it is not. If you deny that it is, you simultaneously admit that *non-material* influences—yes, *im-material, metaphysical* agencies have cooperated in bringing about the result. Take whichever horn of the dilemma you please.

Mind and personality are considered as true "emergents," using the following concept of "emergence" (the author is here referring to perception):

> a *fusion of the potentials* of the antecedent mental experiences, and because such *integrations* are, self-evidently, the very reverse of *differentiations* or *evolutions*—involving the formation of new integrals rather than the 'unfolding' (*i.e.* 'evolution'), actualization or differentiation of the potentials inherent in an already existent integral; and because (in the very nature of things) no mere continuation of a process of pure differentiation can ever in any finite time, result in a process of integration or any process of continued unfolding (evolution) result in a process of enfolding (involution), it is perfectly clear that such integrations and their products, are not the results of Evolution at all, but of external agencies—*i.e.*, agencies foreign to the evolutionary process, and operating in a manner directly opposite to that in which the inherent energies involved in the respective antecedent evolutions are seen to operate.

The author possesses an extensive acquaintance with the literature of the biological sciences, and manages to use it with considerable acuteness.

It is of interest to note that the second chapter opens with the following lines: "Bitterly hostile to Christianity, impatient of criticism, and undoubtedly given to exaggeration Haeckel is, nevertheless, one of the most original, philosophical, and interesting of all the biologists. The author frankly admits that of all writers on Evolution, Haeckel and Huxley are to him the most fascinating."

For the benefit of the pious we would like to point out that the Rt. Rev. Theo. Bratton, Bishop of Mississippi, thinks very highly of the book.

THE EMERGENCE OF HUMAN CULTURE.

By Carl J. Warden. The Macmillan Co., New York. $2.00. 7⅞ x 5⅛; x + 189; 1936.

The author has a great deal to say about the meaning of culture, the biosocial status of animals (social insects, birds and higher mammals), the evolution of culture, and culture and progress. In the section on the emergence of human culture he analyzes the manifold conditions under which man and culture finally emerge, giving a "brief description of the structural and biosocial characteristics of the anthropoid ancestors of man and the great apes" and discussing the "common heritage of the pro-human and pro-ape stock from this earlier primate level," the "further evolution of the pro-human stock from this generalized anthropoid level onward," and "how man and culture emerge from the biosocial matrix of the advanced pro-human level." Just how all this actually happened, however, nature seems to have artfully concealed from inquisitive man a long time ago. The volume contains a bibliography, and author and subject indices.

OBJECTIVE EVOLUTION.

By Christopher Pleydell-Bouverie. Williams and Norgate, London. 7s. 6d. 8½ x 5½; 233; 1936.

"This work presents a politico-cosmological ideal whose aim is the evolution of the efficiency of psychic reactions to the status of sense," according to the author in his preface. Naturally, he has to analyse every phase of our civilization. The causes of the world depression are shown, how biologists should regard heredity and environment, how sex should be taught in school and anything else you happen to think of. Finally he explains that most of the world's problems can be solved by a "consumer's monetary expansion policy" much like the Alberta Social Credit Plan. The remaining problems, such as education, are solved separately. Surprisingly enough some few passages are well worth reading.

ABSTAMMUNGSLEHRE UND DARWINISMUS. *Siebente Auflage.*

By Richard Hesse. B. G. Teubner, Leipzig. 4.20 marks (Germany); 3.15 marks (outside Germany). 9 x 6⅛; iv + 108; 1936.

This little book, the outgrowth of six popular lectures delivered by the author in 1901 on the theory of evolution and natural selection, is now in its seventh edition and still maintains its popularity. Its aim is to make evolution clear to the

layman. The volume is well illustrated and brought up to date with respect to recent thought on inheritance.

GENETICS

METHODIK DER MEDIZINISCHEN ERBFORSCHUNG. *Unter besonderer Berücksichtigung der Psychiatrie.*

By Bruno Schulz. Georg Thieme, Leipzig. M. 10.50 (paper); M. 12 (cloth). 10 x 6¾; 189, 1936.

This book on statistical methods as applied to problems of the inheritance of diseases is addressed particularly to workers in the field who feel shy toward mathematics. Therefore it is written in a manner easily understood by a person not specially trained in statistical procedure. Throughout the book examples are given to demonstrate both correct and incorrect methods. A commendable feature is that the theory of probability is developed more extensively than in most elementary statistical textbooks.

The arrangement is in four parts. In the introduction the author stresses the importance of the use of statistics in the solving of problems involving hereditary traits. This is followed by a section on the collection of data (including twin series and other types of comparative data), and sources of error. In the third part are discussed practically all of the current methods of working out and deriving conclusions from the data collected, together with methods of testing the correctness and significance of results. The final section discusses genealogical investigations and also contains a summary of the most important points in the book.

The nine-page bibliography contains a short list of textbooks and journals on human and general genetics and a longer documentation of the book, arranged by topics of the individual chapters. There is an index.

LES BASES SCIENTIFIQUES DE L'AMÉLIORATION DES PLANTES (*Biologie—Génétique—Écologie—Biométrie—Statistique*). *Encyclopédie Biologique XIII.*

By F. Boeuf. Paul Lechevalier, Paris. 140 francs. 10 x 6½; iv + 543; 1936 (paper).

This book, primarily devoted to Tunisian needs, is divided into three major parts. The first is devoted to a brief exposition on living matter, cellular structure, and the reproduction and multiplication of plants. The laws of heredity, the principles of evolution, and an exposition of the biomorphological basis of plant systematics constitute the second part. The third part is devoted to the scientific basis of plant amelioration: selection, different ways of plant reproduction, adaptation of plant cultures to different physical and chemical environments and the control of results by using comparable scientific methods are discussed.

On the whole, there are relatively few new scientific facts, since the primary aim of the book is to present in a comprehensive way the scientific basis of modern plant culture.

EL DESARROLLO Y LA RELACIÓN NUMÉRICA ENTRE LOS SEXOS EN LOS HÍBRIDOS INTERESPECÍFICOS OBTENIDOS POR FECUNDACIÓN ARTIFICIAL EN EL GÉNERO *TRITON* (*MOLGE*).

By Käte Pariser. Museo Nacional de Ciencias Naturales, Madrid. 9⅝ x 6¾; 93 + 1 plate; 1936 (paper).

In this book are given the results of experiments on the development of sexual characters and the sex ratio in the offspring obtained in the natural manner and by artificial fertilization and crossing of the four species of *Triton* indigenous to Germany—namely, *taeniatus*, *palmatus*, *alpestris* and *cristatus*. With the exception of the crosses between *taeniatus* and *palmatus* the offspring from the various combinations of parents were influenced in color and size by the male parent. The *taeniatus-palmatus* and the *palmatus-alpestris* crosses resulted in a 50-50 distribution of males and females in the first generation offspring, whereas with the others the females predominated more and more in successive generations. In some cases only 1.45 per cent of the individuals were

males. A summary in German and a six-page bibliography are provided.

GENERAL BIOLOGY

BIOLOGICAL EFFECTS OF RADIATION. *Mechanism and Measurement of Radiation, Applications in Biology, Photochemical Reactions, Effects of Radiant Energy on Organisms and Organic Products. Volumes I and II.*

Edited by Benjamin M. Duggar, with the Cooperation of Janet H. Clark, Kenneth S. Cole, Farrington Daniels, Gioacchino Failla, Charles Packard and Henry W. Popp. McGraw-Hill Book Co., New York. $10.00. 9 x 6; xvii + 1343; 1936.

There was a time when the study of light and radiation belonged exclusively in the province of the physicist. Then, at the turn of the century, the biologist entered the picture in a mild way and interested himself primarily with light as a factor in animal behavior. Since that time the field has developed rapidly and today radiation studies from the biological viewpoint represent a lusty department of modern biology and medicine in which many competent investigators are actively engaged. This fact is amply attested by the important two volume book, produced under the auspices of the Committee on Radiation of the National Research Council, here under review. This is a book replete with many authoritative data, theoretical interpretations and extended bibliographies all prepared by experts and dealing with such diverse topics as photons and electrons; measurements of X-rays and radium; ionization and its bearing on biological phenomena; photochemistry; mitogenetic rays; statistical treatment of radiation data; radiation effects on proteins, vitamins, embryonic development, regeneration, protoplasm, behavior of the organism as a whole, various kinds of plants, growth, mutations, bacteria, enzymes, etc., etc. As a whole, the standard of the work is high and the volumes should carve for themselves a long-time niche among scientific reference books. As is inevitable with compendiums of this kind there exists little real correlation between particular sections, and each chapter actually represents a distinct essay dealing with one phase of radiation phenomena. The book is adequately illustrated, briefly indexed and cites an admirable number of pertinent references.

L'OEUF. *Essai de Théorie de sa Segmentation.*

By G. Monteil. G. Doin and Cie., Paris. 18 francs. 9 x 5½; 68 + 16 plates; 1936 (paper).

This is a study of the geometrical principles underlying the process of segmentation, using as examples, for the most part, the eggs of the amphibians and annelids. The theoretical development is extremely condensed, the numerous diagrams to illustrate it so complicated as to be of not the greatest help, and the subject itself a very abstruse and difficult one. The fundamental bases of the theoretical discussion are (1) that, except for eggs of very unequal segmentation, at the anaphase the asters will reach the centres of gravity of the blastomeres in process of formation, the points at which the nuclei will be found at the telophase. (2) For all phases where segmentation is in parallels of the egg sphere, the axes of the spindles will never be vertical, and the planes of segmentation never horizontal. From these bases a series of consequences are deduced, well worth the consideration of embryologists and those interested in the shape of cells in multicellular organs and tissues. An important but difficult book.

T. H. HUXLEY'S DIARY OF THE VOYAGE OF H. M. S. RATTLESNAKE.

Edited from the Unpublished M.S. by Julian Huxley. Doubleday, Doran and Co., Garden City, New York. $3.00. 9 x 6; xiv + 301 + 13 plates; 1936.

"Not events merely but those which influence a man, are of importance." This line from the recently found manuscript diary of Thomas Henry Huxley is a cue to the spirit in which this journal—a record of four years spent as assistant-surgeon and

naturalist aboard H. M. S. Rattlesnake—was kept. The scientific enterprises of this period which won him his place as fellow in the Royal Society at the age of twenty-five are not treated at great length here, but it is of interest to follow his moods and watch the play of his mind in evaluating himself and his work at this time. It was a period of great turmoil, particularly after he met and fell deeply in love with Henrietta Heathhorn who was to become his wife nine years later. During the fourth voyage the emotional upheaval had somewhat subsided, and here we have interesting accounts of islands visited with vivid word pictures of native life and customs. The book is illustrated with sketches and scientific drawings by Huxley, and a few photographs.

ZEIT-ORDNUNGSFORMEN DES ORGANISCHEN LEBENS. *Bios, Band 5.*

By E. Ungerer. Johann Ambrosius Barth, Leipzig. 4.50 marks. $9\frac{1}{4}$ x $6\frac{1}{4}$; vi + 72; 1936 (paper).

The author discusses the rôle of time in organic life, beginning with a comparison of aging, death, and reproduction in one-celled and many celled organisms. He then discusses the periodic organization of organic events as the life cycles of many animals and plants, periodic reproduction phases, etc. Less clear and more speculative is the third section on periodic forms of behavior among animals and man. A short section dealing with the comprehension of time and the ability to save time by means of a feeling of an "inner clock," leaves one rather mystified. The author tends to ally himself with the vitalistic philosophers.

SOCIAL BIOLOGY. *A Textbook for Secondary Schools.*

By Everett P. Walton and Philip E. Foss. P. Blakiston's Son and Co., Philadelphia. $1.68. $7\frac{7}{8}$ x $5\frac{1}{4}$; xv + 537; 1936.

In our opinion there is not the smallest reason for giving this good, but in no way extraordinary, high school text book of biology the title *Social Biology*. In fact to do so verges a bit closely upon misrepresentation. The book contains no more, and essentially no different, material about man than do many other secondary school texts in biology at the present time. And perhaps if the authors had read William Morton Wheeler's famous paper *Termitodoxa* they would not have headed the last section of their book with the words: "Man is the only animal with a social heritage."

ELEMENTS OF GENERAL BIOLOGY.

By Henry R. Barrows. Farrar and Rinehart, New York. $2.60. $8\frac{1}{8}$ x $5\frac{1}{2}$; x + 435; 1936.

This volume was practically completed before Dr. Barrows' death last summer. While based on his larger book, it is in no sense an abridgement since much of the purely morphological material is omitted, some of the sections (especially those in chemistry and physics of protoplasm) have been simplified, and many other changes in the handling of the material and illustrations have been made. In a group of appendices are given a brief classification of plants and animals, notes on vitamins, brief biographical skeletons of biologists of the past, a bibliography and a glossary. The volume is indexed.

FOUNDATIONS OF BIOLOGY. *Fifth Edition.*

By Lorande L. Woodruff. The Macmillan Co., New York. $3.50. $8\frac{1}{2}$ x $5\frac{5}{8}$; xiv + 583; 1936.

The third and fourth editions of the Foundations of Biology have been mentioned in previous numbers of the Q. R. B. (Vol. 3, No. 1 and Vol. 6, No. 1). The present edition has been thoroughly revised, new material has been added, especially in the field of genetics, and there are many new illustrations. Two additional chapters, give a synoptic view of the plant and animal kingdoms. The view point of the earlier editions has been strictly adhered to—namely, to present a

broad survey of the fundamental principles of biology for the college student and the general reader.

MANUAL OF BIOLOGY. *Fifth Edition.*
By George A. Baitsell. The Macmillan Co., New York. $2.50. 8½ x 5⅝; xi + 434; 1936.

In this fifth edition of a well-known laboratory manual a considerable amount of new material has been added, especially in connection with plant types (notably the algae, colorless plants and seed plants). On the animal side, the grasshopper has been added as a type form and the treatment of the vertebrate extended. In many of the chapters a section on *Related facts of importance* has been included for the interest of the more advanced student. The volume contains twelve plates, each chapter is documented and there is an index.

COMPARAISON ENTRE LA RYTHMICITÉ DES COURANTS D'ACTION CELLULAIRES CHEZ LES VÉGÉTAUX ET CHEZ LES ANIMAUX. *Actualités Scientifiques et Industrielles, 314.*
By Daniel Auger. Hermann et Cie, Paris. 20 francs. 10 x 6½; 101; 1936 (paper).

This number of the *Actualités* series is an important contribution in the field of electrophysiology. The author has made an extensive study of the pulsating phenomena of plant tissues, using mainly *Nitella* and *Chara*, and compared their rhythmic behavior to that of animal tissues. Comparison showed that "in spite of the diversity of the rhythms and the variety of origin of the cells on which they were observed, the pulsating systems showed a great unity of behavior."

DEEP SEAS AND LONELY SHORES.
By W. Lavallin Puxley. E. P. Dutton and Co., New York. $2.50. 8 x 5½; 215 + 4 plates; 1936.

A wealth of information is contained in this interesting book. The author has wandered extensively all over the world and he writes for the general reader, who is especially interested in natural history and popular science, of what he has observed concerning the many beautiful and weird creatures that inhabit the seas in many out of the way places. Four illustrations are included in the volume but there is no index.

COLLEGE BIOLOGY.
By Walter H. Wellhouse and George O. Hendrickson. F. S. Crofts and Co., New York. $3.00. 8½ x 5½; viii + 381; 1936.

This is a textbook designed more for "the general student" than for the future biologist, and as such, is fairly well composed. However, we do not feel that thirteen pages of generalized discussion is enough to devote to the entire Phylum Arthropoda in a college course in biology. The bibliography is poor.

ATMOSPHERIC POLLUTION OF AMERICAN CITIES FOR THE YEARS 1931 TO 1933 *with Special Reference to the Solid Constituents of the Pollution. U. S. Treasury Department. Public Health Service. Bulletin No. 224.*
By James E. Ives, Rollo H. Britten, David W. Armstrong, W. A. Gill and Frederick H. Goldman. United States Government Printing Office, Washington. 10 cents. 9⅛ x 6⅞; iv + 75 + 1 plate; 1936 (paper).

This study indicates that atmospheric pollution is greater in winter, on weekdays, and when the wind velocity is low. There is great variation at different times of day but "aside from the morning maximum, the density of the pollution during the day appears to depend largely on the vertical air currents." Rain does not cause a decrease in atmospheric pollution. A useful volume for the ecologist to have on his shelf.

FLOODS IN THE UNITED STATES. *Magnitude and Frequency. U. S. Department of the*

Interior, Geological Survey. Water-Supply Paper 771.

By Clarence S. Jarvis and Others. Prepared in collaboration with the Water Planning Committee of the National Resources Board and its predecessor the Mississippi Valley Committee. U. S. Government Printing Office, Washington. $1.00. 9⅛ x 5⅞; 497 + 3 folding plates; 1936 (paper).

Numerous tables are given concerning the flood peaks and other flow characteristics of flood rises for the various river basins both in the eastern and western parts of the United States. The data are subjected to an extended statistical analysis. Again a useful treatise for the ecologist.

HUMAN BIOLOGY

CORAL GARDENS AND THEIR MAGIC. *A Study of the Methods of Tilling the Soil and of Agricultural Rites in the Trobriand Islands. Volume 1, The Description of Gardening; Volume 2, The Language of Magic and Gardening.*

By Bronislaw Malinowski. American Book Company, New York. $8.00 per set. 9¼ x 6; Vol. 1, xxxv + 500 + 69 plates + two folding maps; Vol. 2, xxxii + 350; 1935.

Malinowski says that this book "is the best I have produced or am ever likely to produce." It certainly is a masterpiece, and, if he feels that way about it, it may well stand as the crowning work of a great anthropologist—in fact now one of the world's foremost.

The first volume is analytically descriptive of the objective phenomena of Trobriand agriculture. The second volume divides itself between the setting forth of an ethnographical theory of language, and a *Corpus Inscriptionum* that is the whole work's basic documentation.

In the space available we cannot convey to the reader the scope and meaning of the book any better or more concisely than in Malinowski's own words.

In this book we are going to meet the essential Trobriander. Whatever he might appear to others, to himself he is first and foremost a gardener. His passion for his soil is that of a real peasant. He experiences a mysterious joy in delving into the earth, in turning it up, planting the seed, watching the plant grow, mature, and yield the desired harvest. If you want to know him, you must meet him in his yam gardens, among his palm groves or on his taro fields. You must see him digging his black or brown soil among the white outcrops of dead coral and building the fence, which surrounds his garden with a "magical wall" of prismatic structures and triangular supports. You must follow him when, in the cool of the day, he watches the seed rise and develop within the precincts of the "magical wall", which at first gleams like gold among the green of the new growth and then shows bronzed or grey under the rich garlands of yam foliage.

The side of tribal life described in these volumes is perhaps less sensational than the sailing and trading and witchcraft known to the readers of the *Argonauts of the Western Pacific*; it may have less direct appeal to our curiosity than the customs of courtship and marriage treated in *The Sexual Life of Savages*. But it is at least as important for our knowledge of the Trobrianders, of Oceanic civilisations and, I venture to say, even of human nature in general.

For, on the one hand, nothing bears so directly on man's economic nature as the study of primitive forms of tilling the soil. The manner in which so-called savages produce their primary sustenance, store it and handle it, the way in which they surround it with magical and religious beliefs, open problems of the relation between man and environment of some importance to economic philosophy. On the other hand, agriculture and its consequences enter very deeply into the social organisation of our South Sea community—and of any community for that matter; they form the foundation of political power and of domestic arrangements; they are the mainstay of the obligations of kinship and of the law of marriage. Thus in many ways the perusal of the present book may add to our knowledge of primitive economic organisation, political order, and domestic life.

THE RELATION BETWEEN MORALITY AND INTELLECT. *A Compendium of Evidence Contributed by Psychology, Criminology, and Sociology.*

By Clara F. Chassell. Teachers College, Columbia University, New York. $4.50. 9 x 6; xviii + 556 + 1 folding chart; 1936.

This volume represents an investigation covering many years of work. It incorporates the material of a dissertation presented in 1920 (entirely rewritten), includes additional data, and introduces certain refinements in the presentation and in the statistical treatment. Many important studies published since the original thesis appeared have been included in the study. These have been subjected to a "uniform tabular method of report, synthesized and merged in a compilation of the correlational results of the research

as a whole." The general subjects dealt with include delinquency and mental inferiority, moral character and intelligence, moral and intellectual traits, conduct and intelligence and a consideration of factors which effect results.

The author finds that

> The relation between morality and intellect in restricted groups is clearly direct. The obtained relation is extremely variable, but tends to be low. The true relation is undoubtedly higher than the obtained relation, but apparently at best it tends to be only marked and frequently it tends to be low. Expressed in correlational terms, the obtained relation may therefore usually be expected to fall between .10 and .39, and the true relation to be under .50." It is believed that "Undoubtedly the relation between morality and intellect in the general population is considerably higher than that usually found in restricted groups. Nevertheless, it is hardly probable that this relation is high. Expressed in correlational terms, the relation in the general population may therefore be expected to fall below .70.

Much tabular material is included in the text and a good deal of supplementary material is added in four appendices. There is a bibliography of 214 titles and an author and a subject index.

THE HERITAGE OF THE BOUNTY. *The Story of Pitcairn Through Six Generations.*
By Harry L. Shapiro. Simon and Schuster, New York. $3.00. 9 x 5⅞; xv + 329; 1936.

The mutiny on the Bounty started no differently than many another difference of opinion between masters and men aboard ship, but in the end it produced the world's tidiest and most interesting experiment in human biology to date. Thanks to the painstaking research and literary skill of Messrs. Nordhoff and Hall everyone just now knows the main features of the story of Pitcairn Island. Dr. Shapiro caps the climax by going to Pitcairn and studying the present-day descendants of the mutineers, with all the refined technique of the modern physical and social anthropologist. An experiment in human race crossing has been as adequately dealt with as is possible under all the cricumstances.

The present volume is a popular account of Dr. Shapiro's experiences and some of the results. More technical reports will appear elsewhere later. He has done an excellent job in this book. His literary skill charms and fascinates as well as informs, and his illustrations are superb—so much so that the only pity is that there are not more of them.

Space is lacking to discuss the many points of extraordinary interest brought out in the book. One, however, we must mention; the decline in fertility. The following table gives the facts for all women who lived to 45 and were married up to that age.

Birth Year of Mother	*Number of Women*	*Average Number of Children per Female*
1790–1814.....	1	6.0
1815–1839.....	5	11.4
1840–1864.....	8	8.0
1865–1889.....	20	5.0
1890–1914.....	2	2.5

Dr. Shapiro rather leans to the view that venereal disease may have played a significant rôle in this fertility decline. It seems certain that contraception did not, though conceivably it may have had some small part in bringing about the observed result.

The book is well indexed, and we recommend it unreservedly.

THE SQUATTING AGE IN AUSTRALIA 1835–1847.
By Stephen H. Roberts. Melbourne University Press, Melbourne. 21s. 8½ x 5½; x + 455; 1936.

Between 1835 and 1847, Australia was transformed from a penal colony to the most important wool producing country in the world. Credit for the transformation is due to the foresight and ability of a few large land-owners and the daring and persistence of the so-called squatters. These were men of all classes and conditions who defied the laws and the opposition of the existing land-owners, went out into the wild country and settled on extensive tracts of forbidden land and raised sheep on a large scale. The author portrays vividly and, at times, with unbecoming passion, the interplay of political, social and economic factors

which centered around the squatting movement. As seen by him, on the one hand there were the authorities in England, mostly theorists with little knowledge of the needs of the colony, who cooperated little with and impeded greatly any intelligent attempt of the local governors to aid the progress of the colony. The governors, on the other hand, were forced to battle the local politicians in the service of the large proprietors who were interested in their own financial well-being. The main point of contention was the question of whether an individual had the right to occupy and keep land that belonged to the Crown. And of course those who had land were for a strict observance of the laws. While the political struggle raged the squatting movement went on. The author brilliantly traces the evolution of the squatter; first a vilified interloper and finally a staunch defender of the *status quo* against the newcomers seeking gold. In the meantime the local governors and the ministry in England blundered along only to be forced, after a number of years, to acquiesce to a state of fact.

While one may not always agree with the author's interpretations, nevertheless he succeeds in showing effectively the futility of laws and pre-determined regulations when they seek to put a limitation to one of the most important human activities, that of making a living; or attempt to stop what was once called social capillarity.

INSTITUTIONAL TREATMENT OF DELINQUENT BOYS. *Part 2. A Study of 751 Boys. U. S. Department of Labor. Children's Bureau Publication No. 230.*

By Alida C. Bowler and Ruth S. Bloodgood. U. S. Government Printing Office, Washington. 15 cents. 9¼ x 6; v + 149; 1936 (paper).

This is the second part of a report on 751 delinquent boys who were committed for some time to State Institutions in either California, Michigan, New Jersey, New York or Ohio. (The first part of this report was reviewed in Q. R. B. Vol. 10, No. 4, 1935.) Here the authors present statistical data regarding (a) pre-committment history of the boys: age, home and environmental conditions, type of offense; (b) institutional treatment: vocational training, conduct, etc.; (c) conduct of the boys on parole and after leaving the institutions. Information regarding this last item is of particular importance because from it one can judge the value of institutional care. It is sad to learn that 77 percent of the boys did not or could not utilize the trade learnt in the institution. Moreover, the majority of the boys about five years after their release from the institutions, were earning very low incomes. In relation to this, the authors note that of 10 percent of the boys earning average incomes or better, a number derived their high income from illegal enterprises. The most significant fact observed in this investigation is that 66 percent of the boys for whom information was available, had been arrested once or more since their release from the institution and that 42 percent had been committed to some penal institution.

While these findings are not altogether new, they demonstrate again that something is definitely wrong with the method by which these sample institutions attempt to educate and reform the children. The authors are aware of this but nevertheless limit themselves to mild ineffectual criticism.

KENYA. *Contrasts and Problems.*

By L. S. B. Leakey. Methuen and Co., London. 7s. 6d. 7¼ x 5; xiii + 189 + 8 plates; 1936.

The author, who was born in Kenya and has acquired a considerable knowledge of the country and its peoples from his anthropological studies there, does not see eye to eye with the British administration of this territory. In the first place, he believes that conflict with the natives arises from the fact that the British administrators do not understand the point of view of the natives nor are the local Colonial officials given a chance to learn. In the second place, it is evident that as the education of the natives proceeds they will demand more and more

political rights and this will augment the tension already existing between natives and the white settlers. In the author's opinion, it will be better for the white settlers engaged in agricultural enterprises to return to England and leave the land to the natives. He observes that the physical aspects of the country are changing in a way unfavorable for modern agricultural methods and therefore the white men will suffer while the natives with their "uncivilized" methods can still use the soil to great advantage. Only in the development of the mineral resources will the white man obtain the greatest profit from this country with benefit to England and the natives of Kenya.

The book is engagingly written and contains excellent chapters on the physical aspects of the country and its geologic formations; on the means of traveling; and on the missionary work.

BALUBA ET BALUBAÏSÉS DU KATANGA.

By Edmond Verhulpen. L'Avenir Belge, Anvers. 150 francs (paper), 180 francs (cloth) in Belgium; 175 francs (paper), 210 francs (cloth) outside of Belgium. 10 x 6½; 534 + viii + 2 folding maps; 1936.

The legends and traditions of the natives constitute the sources from which the author derives this outline of the political history of the Baluba tribes that inhabit the Belgian Congo. Sometime in the 15th century the Balubas invaded this region and established an empire. This history begins from that epoch and the author traces the fortunes of the rulers of the region from that period to the present day. He includes brief notes regarding their achievements, the forms of government, the administrative subdivisions, the titles of the officials and their prerogatives and functions. No one can doubt that obtaining these data was a formidable task. Regarding their accuracy, the author points out that the dates and facts as he notes them are internally consistent as to chronology, and are in agreement with the reports of the early explorers and administrators of this and contiguous regions. The author himself was at one time administrator of the Belgian Congo, and this book is written in the style of an official report. Very little is mentioned about the ethnology of these peoples, but the author includes a small vocabulary, genealogic charts and excellent maps.

To the human biologist and sociologist, in particular, this book will be welcome especially because of its extensive bibliography on the subject of the Balubas.

GEOGRAPHY. *An Introduction to Human Ecology.*

By C. Langdon White and George T. Renner. D. Appleton-Century Co., New York. $4.00. 8¾ x 6; x + 790 + 1 folding chart; 1936.

An important text book for college and university students which embodies all the important advances that the study of geography has made in recent years. In brief it is a study of man's conquest of the land and water of the earth, of the losses to which the natural resources are being subjected through mismanagement, and of the methods by which these can be conserved. It includes also the economical, social and political reactions of man in different environments. The volume is divided into ten parts. The first deals with human ecology and the geographical elements, then follow sections on the climatic factor (11 chapters); the biotic factors (2 chapters); the physiographic factor (4 chapters); the edaphic factor (2 chapters); the mineral factors (3 chapters); the hydrographic factors (3 chapters); spatial factors (5 chapters); the geographical unit (4 chapters); and the social factor (1 chapter). The volume is generously illustrated with photographic reproductions, charts and maps, and has an excellent working index. The senior author is professor of geography in Western Reserve University and the junior author is senior economist of the U. S. National Resources Committee.

THE MEDICAL DICTATOR AND OTHER BIOGRAPHICAL STUDIES.

By Major Greenwood. Williams and Norgate, London. 7s 6d. 7¾ x 5¼; 213 + 6 portraits; 1936.

This volume of essays is not only a notable contribution to medical history but also to *belles lettres*, for Professor Greenwood, the distinguished medical statistician, has literary talents far above those of scientific men generally. The discussion is of seven men, of whom six were more or less important figures in the history of medicine—Galen, John Freind, Peter Mere Latham, William Farr, Pierre Charles Alexandre Louis, and William Osler—while the seventh was Greenwood's great and good friend Arthur William Bacot, an amateur entomologist, who became a professional only in the last few and happiest years of his life, only to meet an untimely end from an accidental laboratory infection with typhus, on which he was working experimentally at the time.

The charm of these essays cannot be conveyed in a review. It can only be got by reading them. We warmly recommend that this be done.

REINE UND ANGEWANDTE SOZIOLOGIE. *Eine Festgabe für Ferdinand Tönnies zu seinem achtzigsten Geburtstage a m 26. Juli 1936.*

By Albrecht, Boas, Bohnstedt, Bosse, Brenke, Baron v. Brockdorff, Colm, Günther, Harms, Heberle, Hermberg, Jahn, Jurkat, Kanellopoulos, Löwith, Meinecke, Niceforo, v. Reichenau, Schmalenbach, Sorley, Sorokin, Steinmetz, Stoltenberg, Takata, Thurnwald, Wernicke, v. Wiese, Wilbrandt. Hans Buske, Leipzig. 12.37 marks. 9¼ x 6½; 403 + 1 plate; 1936 (paper).

This symposium of current sociological thought, was occasioned by the 80th birthday of Ferdinand Tönnies, the eminent German sociologist, to whom it has been presented in token of his contributions to sociology. After an introduction by von Wiese, discussing present day trends in sociology, the material is assembled in five sections. Part I deals in general with the history of sociology; Part II with theoretical sociology, systems and methods, and theories of social structure; Part III with empirical sociology and sociography; and Part IV with race theories and philosophy. Part V contains three articles on the life and works of Tönnies.

The majority of the authors are German professors, but besides these there are contributions from distinguished sociologists of America, England, Norway, Japan, Italy, Greece and Holland. Two of the 28 papers are in English. The rest were either originally written in, or have been translated into German.

LES RACES HUMAINES.

By P. Lester and J. Millot. Armand Colin, Paris. 10.50 francs (paper), 12 francs (bound). 6⅞ x 4¼; 223; 1936 (paper).

The first part of this book, written by the senior author, is concerned with physical anthropology. In it he discusses the physical characters of importance for anthropologic investigations, presents a classification of races and describes the characteristics which differentiate the several racial groups. Included is also a chapter on pre-historic man.

In the second part of the book, dedicated to physiological anthropology, the junior author outlines the results of comparative studies on growth, blood types, basal metabolism, development of nervous system, etc. In the concluding chapter the authors discuss the subject of pure races and racial mixtures. They point with pride to the fact that the French people have always remained aloof from the violent debates on the question of racial superiority which, they emphasize, the German people and the Anglo-Saxons of the United States use for political purposes.

Although the bibliography is far from complete, the student interested in human biology will find this little book very useful because it contains much information accurately and clearly related.

FAMILY BEHAVIOR. *A Study of Human Relations.*

By Bess V. Cunningham. W. B. Saunders Co., Philadelphia. $2.75. 7¾ x 5¼; 471; 1936.

The purpose of this book is to give the college student a general view of the problems concerned with inter- and intra-familial relations. The author discusses the influence of different social and racial origins on the behavior of the members of the family and of the family with its neighbors, the clash of contrasting individual personalities, the education of children, and so on. In fact, every aspect of family life is here studied, but with varying degree of completeness depending on whether the author had at her disposal, for a particular question, the results of psychological and social investigations. The merit of this book lies just in the thoroughness with which she has surveyed the literature on the subject, the extensive bibliography she presents and her ability to interpret the studies she cites. However, for those topics regarding which there are available few or no facts, the author's discussions become very superficial and somewhat resemble the newspaper columns of a Dorothy Dix or Beatrice Fairfax.

ALIEN AMERICANS. *A Study of Race Relations.*

By B. Schrieke. The Viking Press, New York. $2.50. 8⅛ x 5½; xi + 207; 1936.

This volume analyzes and elucidates the problems of certain alien peoples in the United States. The author, a graduate of the University of Leiden, and with 18 years experience in educational affairs in Dutch East Indies, was invited by the Julius Rosenwald Fund to make the survey. During the year that he devoted to this study he informed himself with considerable thoroughness on the Negro problem in the South, on the situation of the Chinese and Japanese in California, and the Mexicans and Indians in the Southwest. In an appendix he discusses Filipino immigration. The larger part of the book is devoted to the southern Negro, particularly his status from the time of the Civil War up to the present.

The student of American race problems will find little that is new in these pages. The chief value of the book probably lies in the fact that the general reader has at hand a clear and accurate setting forth of the conflict of races in the South and Southwest. The volume is documented and indexed.

WARNING FROM THE WEST INDIES. *A Tract for Africa and the Empire.*

By W. M. Macmillan. Faber and Faber, London. 8s 6d. 8 x 5¼; 213 + 1 folding map; 1936.

Professor Macmillan's description and analysis of social, economic, and political conditions in the West Indies is exceptionally clear and logical. The problem arises from both the economic and the racial situation, the former, he believes, being the major key to the solution of the latter. Professor Macmillan's personal political philosophy naturally conditions the sort of warning he gives. He believes that the economic prosperity as well as the political and social freedom of the colored peoples of Africa and the West Indies are quite as important as those of the whites. Moreover, he thinks it is up to England to do something about it. The danger is that the colored population will not be able to develop into a strong independent peasantry due to the lack of interest if not positive oppression of the whites; and that, therefore, the whites themselves will eventually fail financially and degenerate culturally. His solution is greater coöperation on a more equal footing to secure more efficient agricultural methods.

MORE PROFIT THAN GOLD.

By Joan Arbuthnot. Charles Scribner's Sons, New York. $2.50. 8¼ x 5⅝; 287 + 12 plates; 1936.

An account of surely one of the most completely cockeyed expeditions in search of gold and diamonds ever heard of. To the back country of British Guiana near the eastern border of Venezuela went a party of four Britons, 1♂ and 3♀, of

whom certainly two, maybe three, and perhaps even four could with substantial accuracy be literally described as "babes in the woods." That they did not all die in the jungle appears on the record to have been nothing short of miraculous. They apparently got no gold to amount to anything (the author is uniformly vague about sordid factual matters of a quantitative nature such as dates, etc.). But they had a lot of adventure.

It is a book that any biologist, general or human, is likely to finish if he starts reading it—perhaps because it is so irritating. Its philosophical outlook is basically that of Leicester Square, soaring in its more spiritual moments to that of Picadilly Circus.

ORIENTAMENTO PROFESSIONALE. *Bollettino d'Informazioni. Anno 1, N. 1; N. 2. Edited by Giovanni Scanga. Ministero Dell' Educazione Nazionale, Rome.* 9¾ x 6⅞; 27 pages each, 1935 and 1936 (paper).

These are the first two numbers of a new periodical published by the Italian Ministry of National Education. Its purpose is to diffuse information on the topic of educational and vocational guidance. Reviews and abstracts of articles dealing with psychological investigations on the measure of individual abilities will constitute the most important section of the journal.

In these two numbers, besides the reviews, there are articles on special training courses for teachers recently established in Italy and on the forms to be used in the medical examination of school children made with the object of determining their fitness for special trades. Included is also a report regarding the International Congress of Technical Teachers which was held in Rome, May, 1936.

THE ANATOMY OF PERSONALITY. *By Clements C. Fry and Howard W. Haggard. Harper and Bros., New York.* $2.00. 8 x 5; xi + 357 + 1 plate; 1936.

This is an attempt to analyze, describe and classify human personality. According to the authors, the elements of personality are: the physique, the impulse or driving force, the intelligence, the temperament, the ego. Each of these elements is discussed at length in separate chapters. These also include numerous examples to illustrate the variations and combinations of elements which characterize the different types of "normal" and psychopathic personalities. The outstanding fault of the book is that nowhere do the authors state exactly what they mean by the terms personality, temperament, etc. Aside from this, the book is to be regarded as a well written, interesting, and occasionally amusing popular version of numerous facts and theories regarding the psychological aspect of human constitution.

AFRICA'S GOD. *I—Gold Coast and Its Hinterland. Anthropological Series of the Boston College Graduate School, Vol. I, No. 1. By Joseph J. Williams, S.J. Boston College Press, Chestnut Hill, Mass.* $1.00. 9¾ x 6⅝; 86; 1936 (paper).

The form of early religion and the lines of its development among the natives of the Gold Coast and its hinterland is the subject of this exposition which takes the form of a debate developed by means of quotations from persons who have lived and worked among these tribes and who are therefore considered to be "competent authorities" on the subject.

The conclusion reached is that there is, in general, on the Gold Coast Olympus a Supreme Being with a group of subservient spiritual entities, and another lower group of spiritual entities—the ancestral spirits.

There is a bibliography and author and subject indexes.

HUMAN GEOGRAPHY. *The Pacific Lands. By J. Fairgrieve and Ernest Young. George Philip and Son, London.* 2s. 6d. net. 7⅛ x 4¾; iv + 226; 1936.

Written primarily for use in intermediate

and secondary schools, this text covers briefly for the lands in and surrounding the Pacific Ocean such topics as winds, temperatures, climate, mountains, rivers, vegetation, minerals, foods, people, religions, and occupations. The authors have endeavored to present these facts "in such a way that they are seen to make a little clearer some of the problems of the modern world," and it may be said that their aim has been reasonably achieved.

ZOÖLOGY

THE SPONGES OF THE BAY OF NAPLES, PORIFERA INCALCARIA. *With Analyses of Genera and Studies in the Variations of Species.*

By G. C. J. Vosmaer. Edited by C. S. Vosmaer-Röell and M. Burton. Martinus Nijhoff, The Hague. Gld. 125 (paper); Gld. 135 (cloth). 13¼ x 10; 875 + 69 plates; 1932–1935.

This magnificent monograph is a contribution of major importance to the permanent literature of zoology. It is greatly to the credit of the Dutch that they have financed, at what must have been great expense, the really adequate publication of Vosmaer's remarkable work.

The monograph is fundamentally taxonomic in character. Some 30 odd genera are systematically dealt with. Special attention is devoted to the boring sponges belonging to the family Clionidae. But the work is of deeper import biologically than straightforward taxonomy. Professor Vosmaer was much interested in the problems of organic variation, and includes a great mass of pertinent and significant data on variation in the forms with which he is dealing. Some day this mass of material will be tapped to good purpose by the theoretical biologists studying evolution.

In many ways the oustanding feature of these three volumes is the series of superb plates, mostly in color, and beautifully reproduced from paintings of the living sponges.

Altogether we have here a worthy monument to the memory of a great zoologist. It will stand for a long time as a solid reference work.

ARABIAN ADVENTURE *to the Great Nafud in Quest of the Oryx.*

By Douglas Carruthers. H. F. and G. Witherby, London. 8s. 6d. net. 8¾ x 5½; xii + 208 + 33 plates and 2 maps; 1935.

An extraordinarily interesting book, written in 1934 about a trip into central Arabia in 1909, in successful search for one of the shyest of mammals, the White Oryx of Arabia, first named *Antelope oryx* by Pallas in 1777, and nearly a century later accurately described by John Edward Gray as *Oryx beatrix*. It seems as certain as any such matter can ever be that this creature furnished the factual basis for the fabled unicorn, for while it has two horns, in certain lights and aspects it appears to have but one. The author, a friend of T. E. Lawrence, presents an unusual combination of erudition, love of travel and adventure, and first-rate literary ability.

The Oryx is a strange beast, thoroughly adapted to desert life in the most arid regions and able to survive definitely only because of these adaptations.

> Of water the Oryx are independent, but moisture they must have, and of necessity they follow the pasture that holds it. The most succulent grasses, such as *Nussi* and *Sabat* are doubtless their principal food, but the young shoots of tamarisk and other shrubs are sought for in spring. Even more desired are those peculiar juicy parasites that grow on the roots of the desert shrubs, especially the tamarisk and *ghadha*. There are two sorts, the red *Tarthuth, Cynomonium coccineum*, and the yellow *Phelipea lutea*. These long spadices may be as much as 18 to 24 inches long, and are full of liquid, especially the major portion below the sand. The Oryx dig for these so as to get at the best and most succulent end. Besides these, there are numerous other bulbous and tuberous plants which supply the moisture which these drinkless Antelope must have. Regarding the term "drinkless," some explanation is needed. It is quite obvious that the Oryx, as indeed all animals inhabiting this arid region, must be able to endure indefinitely without a proper drink. In no case is there any possibility of there being surface water, such as rain-pools caught in hollow rocks, for more than a few months in the year. In many districts even this chance of a brief drinking-hour is withheld. The Oryx, therefore, can be said to be entirely independent of water, although they will drink if given the opportunity to do so.

The photographs illustrating the volume are remarkable. There is an excellent bibliography and also an index.

THE FLOUR BEETLES OF THE GENUS TRIBOLIUM. *United States Department of Agriculture Technical Bulletin No. 498.*

By Newell E. Good. U. S. Government Printing Office, Washington. 10 cents. 9¼ x 6; 57; 1936 (paper).

In recent years a rising interest in the flour beetles of the genus *Tribolium* has been apparent. This interest has developed largely within two groups of investigators: the economic entomologists, who have had to cope with the control of these beetles as serious pests in flour mills, and the experimental population students, who have found in *Tribolium* a useful animal for the study of their problems. The present paper by Good is designed to lay certain general foundations about *Tribolium* which will be useful to both of these groups as a background for their work. The author discusses in detail for the first time the taxonomy of the genus and shows, among other things, that the red-rust flour beetle commonly known as *Tribolium ferrugineum* Fabr., is more properly designated *Tribolium castaneum* Herbst. This section is followed by a consideration of the history and economic status of *Tribolium*; a detailed account of the life-cycle of our two American species *Tribolium confusum* and *T. castaneum*; the interrelations of the flour beetles with other animals, and control measures useful in checking *Tribolium* infestations of stored products. A considerable amount of new data appears at various places throughout the text. This is especially true of the section on life-cycles where Doctor Good presents some original records on oviposition and mortality.

To certain people this paper will be welcomed as an important reference work. It summarizes competently a great deal of information about the flour beetles, and, unlike many economic studies, maintains a sound, biological approach throughout. An outstanding feature is the excellent bibliography which lists some 108 titles all directly or indirectly related to *Tribolium*. The illustrations are likewise of high standard.

PAPERS FROM TORTUGAS LABORATORY OF CARNEGIE INSTITUTION OF WASHINGTON. *Vol. XXIX. Carnegie Institution of Washington Publication No. 452.*

Carnegie Institution of Washington. $4.75 (paper); $5.75 (cloth). 10 x 7; 386 + 27 plates; 1936.

Valuable contributions in the field of marine biology are presented in this collection of fourteen papers covering studies on the biology of Tortugas corals; parasitic copepods from the Dry Tortugas; the ciliates of sea-urchins; intersexuality in the crustacea and the mechanism of chela differentiation in the crustacea; regeneration, cytology, metamorphosis of particular marine forms; electrical resistance of *Valonia*; the water exchanges of living cells; the effect of light on orientation and stability of young plectognath fish.

The longest and most detailed report is made by E. M. Thorp on the calcareous shallow-water marine deposits of Florida and the Bahamas. Mechanical analyses to determine the percentages of marine deposits and microscopical analyses to determine the organic constituents were made of 74 bottom samples and the results are listed in tabular form. The largest contribution of organically secreted calcium carbonate was made by the coralline algae. The principal non-calcareous mineral was quartz.

A paper by Oscar W. Richards examines critically the use of the heterogonic constant k in the formula $y = b\,x^k$ when this is employed to represent the growth of a part (y) of an organism with respect to the growth of the rest of the organism (x). Data on the relationship between the size of the larger chela and the body of the male hermit arab *Caenobita clypeatus* are presented to show that a linear regression curve may give a more satisfactory fit than the above formula.

A MONOGRAPHIC REVISION OF THE GENUS CEUTHOPHILUS. (*Orthoptera, Gryllacrididae, Rhaphidophorinae*) *Biological Science Series, Vol. II, No. 1.*

By Theodore H. Hubbell. University of Florida, Gainsville. $3.75. 10½ x 7; 551 + 38 plates; 1936 (paper).

Cave-crickets and camel-crickets are the more commonly known insects of the

genus Centhophilus (sub-family Rhaphidophorinae)—second largest genus of North American Orthoptera.

Rhaphidophorids are generally supposed by entomologists to be uncommon, and are rarely seen by other persons. This is largely the result of their secretive habits; active by night, they spend the day in close concealment. They have no song to attract attention, and are rendered inconspicious by their sober coloration and immobility in the presence of strong light. Most of the species inhabit woodland, seeking shelter among the dead leaves and other debris of the forest floor; others are grassland- or even desert-dwellers, and these commonly dig holes in the ground, or take refuge in the burrows of larger animals or in natural cavities, from which they may emerge on nocturnal forays. Many species find the twilight zone in the entrances of caves a congenial habitat, and in such places these insects often congregate in large numbers.

It is probable that a large number of species are still to be discovered, but the present volume is the only comprehensive treatise on the taxonomic data of the group as known to date, the last account having been published in 1894. Many important changes have been made in classification since that time, and many new species described. The author has indeed produced here a superb piece of sound taxonomic work. There is a good bibliography and an index.

General Entomology.

By Robert A. Wardle. P. Blakiston's Son and Co., Philadelphia. $2.25. 8½ x 5½; vii + 301; 1936.

This small entomological text,

. . . . is intended for students to whom the subject of entomology represents merely one or two courses of the many that comprise their training for the profession of zoölogy or agriculture, and who do not require the detailed knowledge of insect morphology and insect classification that is essential to the professional entomologist, but do require a broad appreciation of the basic principles of the subject.

In general, the book lives up to this standard set in the preface and should find friends among the group for which it is written. Despite its small size the author has succeeded in treating, in moderate detail, most of the important aspects of entomology, *viz.*, anatomy, development (both embryonic and post-embryonic), physiology, behavior, taxonomy and characteristic group features, etc. On the whole the volume leaves the reader with a fairly rounded survey of the subject. A novel, and in some ways courageous, feature of the book is the listing of contemporary entomologists, who are, in the opinion of the author, the recognized authorities in their respective fields. Certain references are cited in the text but no comprehensive bibliography or glossary is included. The illustrations are few and not particularly distinctive.

An Analysis of the *De Generatione Animalium* of William Harvey.

By Arthur W. Meyer. Stanford University Press, Stanford University, Calif. $3.00. 8 x 4⅞; xx + 167 + 11 plates; 1936.

Once an individual acquires prominence in a particular field of activity, it is usually assumed that his judgment is infallible on any other subject. At present, for example, the opinions of eminent astrophysicists on religion, politics and general science are regarded as sacrosanct.

To a much lesser degree the same sort of thing has happened in the case of Harvey. The great discovery presented in the *De Motu Cordis* has been considered a sufficient guarantee that *De Generatione Animalium* is of the same calibre. Huxley regarded it as a "remarkable work which would give him claim to rank among the founders of biological science had he not been the discoverer of the circulation of the blood." In this analysis, Meyer shows that such hyperbolic praise is really not justified. With all due respect to Harvey, the author finds very little to distinguish this treatise from those of Harvey's predecessors or contemporaries. Even the famous phrase attributed to him *Omne vivum ex ovo* is a misquotation. To Harvey's credit it must be said that he avoided a number of the superstitions then in vogue. Still he was unable to perceive the facts of reproduction any clearer than the other investigators of the time.

Harvey's greatness does not suffer from this critical analysis of *De Generatione*. The author at all times maintains a respectful attitude and his criticism is mild and impersonal. For this, he deserves great credit. The book should be required

reading for all science students. Due to the teaching methods still in vogue, most of the students cannot liberate themselves entirely from the awe for a great name.

THE AMERICAN WOODCOCK PHILOHELA MINOR (GMELIN). *Memoirs of the Boston Society of Natural History, Volume 9, No. 2.*

By Olin S. Pettingill, Jr. Boston Society of Natural History, Boston. $4.75 bound; $3.50 paper. 12 x 9½; 225 + 10 plates; 1936.

The American woodcock is a bird well-known in eastern North America as a table delicacy, but perhaps fewer people are well acquainted with its interesting life history. The perusal of this monograph however gives the reader a ring-side seat whereby he can watch as though at first hand the development of individuality in this bird. The courtship performance of the woodcock is unique and is described in detail, and other characteristics are just as adequately treated. This compact assemblage of material is a result of intensive and intimate field studies of the bird, a good review of the literature on the subject, the returns from a thousand questionnaires sent out requesting information relative to abundance, migration and breeding, and the examination of skins and skeletons and dissection of specimens. The monograph is beautifully illustrated.

PIGEONS AND SPIDERS (*The Water Spider*).

By Maurice Maeterlinck. Translated by Bernard Miall. W. W. Norton and Co., New York. $1.75. 7½ x 5⅛; 128; 1936.

This entertaining volume is largely about the Argyronet, a spider that chooses to envelope itself in a "silver" diving bell and carry on its activities mostly beneath the water. Maeterlinck first became acquainted with these spiders when as a boy he observed them in a moat surrounding his grandfather's garden. With his grandfather, who must have been something of a naturalist, he studied them in a "natural history cabinet"—a glass jam pot. Sixty-two years later the writer renewed his interest in these creatures when there happened to reach him from Belgium a jam pot "which bore a magical resemblance to the jam pot of my childhood, and in this too half a dozen bubbles of mercury were in motion, just like those of my premonitory vision." Of equal interest is the essay on pigeons. Maeterlinck cannot resist debunking them somewhat but tells many amusing things about them and discusses their family life, their habits, and sense of orientation. As one would expect both of these essays include philosophical discussions on instinct, intelligence, nature, and life. Many questions are asked, but very few does the author really attempt to answer.

THE INTERPRETATION OF THE ZONES ON SCALES OF SALMON, SEA TROUT AND BROWN TROUT. *Rapports et Procès-Verbaux des Réunions Volume XCVII.*

By T. H. Järvi and W. J. M. Menzies. Andr. Fred. Høst and Fils, Copenhagen. Kr. 4.00. 10¾ x 8¼; 63; 1936 (paper).

The technique of scale reading for age determination of three salmonoid fishes is clearly described in the text of this report and is closely supplemented with photographic illustrations. During the first summer the scale ridges are well spaced and well formed, but thereafter summer is denoted by a wide growth zone and winter by a slow growth zone of finer and more closely spaced ridges. Spawning periods may also be read from the scales. During the ascent of the rivers to the spawning grounds reserves of nourishment stored in the scales are absorbed, thus destroying scale material to a greater or less extent. Normal growth is resumed again on return to the sea. Some of the pitfalls or complications of scale reading are also described. The authors are both recognized authorities in this field of research.

COLLEGE ZOOLOGY. *Fourth Edition.*

By Robert W. Hegner. The Macmillan

Co., New York. $3.50. 8½ x 5½; xvi + 742. 1936.

The fourth edition of this well-known and extensively used zoölogical textbook has been revised by rewriting many of the chapters; by expanding the discussions of the Protozoa, Arthropoda and the frog; by adding new chapters on the "Relations of Protozoa to Man" and on "Parasitism in Animals"; by enlarging the glossary and adding cross-page references to it, and by including a number of new illustrations. It is interesting to note that the author still holds to the "type" method of presentation—the development of the subject from the viewpoint of taxonomic groups. This procedure, once conservative, is now becoming more radical due to the increasing number of books based on "principles"—the organization of the subject about certain concepts and theories. As to which method of presentation is superior it is difficult to say. It can be predicted, however, that this text will continue to enjoy popularity in its fourth edition.

BIRDS OF CAPE YORK PENINSULA. *Ecological Notes, Field Observations, and Catalogue of Specimens Collected on Three Expeditions to North Queensland.*

By Donald F. Thomson. Angus and Robertson, Sydney. 1s. 6d. 9½ x 6; 82 + 15 plates; 1935 (paper).

During the course of expeditions carried out over a period of three years into North Queensland for anthropological work, a study of the birds of the region was made as a side issue, largely from the standpoint of geographical distribution. There is a brief descriptive account of the physical characteristics of the Cape York Peninsula and a classification of the country into five principal flora-fauna association areas. 183 species of birds were observed here. It is interesting to note that less than half of this number are endemic Australian species while the remainder have a range extending to New Guinea or beyond. An index of the common as well as scientific names is included.

SEASHORE ANIMALS OF THE PACIFIC COAST. *By Myrtle E. Johnson and Harry J. Snook. The Macmillan Co., New York.* $6.00. 9¼ x 6¼; xiv + 659 + 11 plates; 1935.

A reprint of a volume which first appeared in 1927. It is a non-technical, illustrated account of the structure and habits of the common seashore animals of the west coast of the United States. Being replete with interesting information and excellently illustrated with numerous line drawings, half-tones and colored plates, teachers of elementary biology in colleges and high schools will find the volume highly useful. Naturalists, particularly those visiting the west coast, will find it a desirable library book. Unfortunately its size and weight do not make it handy for field work. The authors have included sections on collecting and preserving marine forms, a lengthy reference list, a glossary and an index.

LEÇONS DE ZOOLOGIE. *Protozoaires flagellés. Actualités Scientifiques et Industrielles, 296.*

By M. Prenant. Hermann et Cie, Paris. 12 francs. 10 x 6½; 56; 1935 (paper).

LEÇONS DE ZOOLOGIE. *Protozoaires infusoires ciliés. Actualités Scientifiques et Industrielles, 295.*

By M. Prenant. Hermann et Cie, Paris. 15 francs. 10 x 6½; 77; 1935 (paper).

These two books, members of the rather lengthy series surveying the invertebrates, present certain orthodox taxonomic, morphological and physiological data on the flagellate and ciliate Protozoa. As with previous volumes the standard, while adequate, is not especially distinctive and one feels that just another textbook discussion of two animal groups has been created. Both books contain a number of mediocre, time-worn illustrations of familiar forms and both have bibliographies of a few selected titles. It seems certain that if these paper-bound brochures get the type of service usually accorded textbooks they will last about one semester if not less.

ZOOLOGICA. *Scientific Contributions of the New York Zoological Society. Volume XXI, Part I, Numbers 1 and 2. Containing following articles: The Reproductive Habits of the North American Sunfishes (Family Centrarchidae)*, by C. M. Breder, Jr.; *Polychaetous Annelids from the Vicinity of Nonsuch Island, Bermuda*, by A. L. Treadwell.

New York Zoological Society, New York. $1.00. 10½ x 7; 68 + 10 plates; 1936 (paper).

Breder's monograph on the sexual and breeding behavior of the common sunfishes is a valuable and important contribution. In addition to his own original observations, which bring out many novel points, he thoroughly and critically reviews the older literature. It is an interesting finding that the primitive forms make the most elaborate nests and give more parental care than the higher forms, where the nests are much simpler.

Treadwell lists and describes 27 old and 8 new species of polychaetes from Bermuda.

OUTLINES OF GENERAL ZOOLOGY. *Third Edition.*

By Horatio H. Newman. Macmillan Co., New York. $3.50. 8½ x 5½; xxvii + 661; 1936.

A LABORATORY MANUAL FOR GENERAL ZOÖLOGY.

By Katherine McC. Roehl in collaboration with H. H. Newman. Macmillan Co., New York. $1.00. 8½ x 5½; vii + 99; 1936.

In this new edition of Newman's standard and successful text "much of the book has been completely rewritten, but a great deal of it remains unchanged" or only slightly modified. Summaries at the end of chapters are a new feature.

The laboratory manual was especially designed for use with the *Outlines* but the authors believe that it should fit any textbook of general zoology or animal biology.

A LABORATORY MANUAL OF INVERTEBRATE ZOOLOGY. *Fifth Edition, Reset.*

By Gilman A. Drew. Revised by James A. Dawson and Leonard P. Sayles. W. B. Saunders Co., Philadelphia. $2.25 net. 7⅝ x 5; 276; 1936.

Rapidly becoming a classic of the invertebrate dissection laboratory, this book (earlier reviewed in Q.R.B., 1929: 4; p. 280) has been revised,

> . . . . for the purpose of modifying and enlarging the fourth edition. Some important changes in classification have been made and the instructions for the study of certain commonly used animals have been made more complete. Such errors as had not been eliminated in earlier editions have, it is hoped, been corrected. The glossary has been thoroughly rewritten and revised.

DIE BLATT-MINEN MITTEL- UND NORD-EUROPAS. *Bestimmungs-Tabellen aller von Insekten-Larven der verschiedenen Ordnungen erzeugten Minen. Lieferung 2.*

By Martin Hering. Gustav Feller, Neubrandenburg. 9⅜ x 6¼; 113–224 + 1 plate; 1936 (paper).

A continuation of an identification list, with some illustrations, of leaf burrows. Arranged alphabetically by plant host this number includes from *Bryonia* (Curcurbitaceae) to *Filipendula* (Rosaceae). The first number of the work was noticed in this REVIEW, Vol. 11, p. 239.

HEDGE FOLK IN TWILIGHT.

By Phyllis Kelway. Longmans, Green and Co., New York. $2.50. 7⅞ x 5½; xi + 178 + 22 plates; 1936.

At one time or another Miss Kelway has made friends with a number of wild creatures such as dormice, hedgehogs, a heron, and a most amusing brown owlet. She now tells us of her experiences in a pleasant, unpretentious way. Her book won't add much to the general body of scientific knowledge, but it is good reading.

A SHELLAC PATENT INDEX.

By R. W. Aldis. Indian Lac Research Institute, Namkum, Ranchi, Bihar and Orissa, India. Rs. 2/8. 9⅞ x 7¼; iv + 115; 1935.

This book gives lists of patents concerning the manufacture and use of shellac. It is clearly arranged and there is a good index.

DINOFLAGELLATA OF THE SAN FRANCISCO REGION. *On the Skeletal Morphology of Two New Species, Gonyaulax Catenella and G. Acatenella. University of California Publications in Zoology. Vol. 41, No. 4.*

By W. Forest Whedon and Charles Atwood Kofoid. University of California Press, Berkeley. 10¼ x 6⅞; 25–34; 1936 (paper).

SPAWNING HABITS OF THE MUSSEL MYTILUS CALIFORNIANUS CONRAD. *With Notes on the Possible Relation to Mussel Poison. Mussel Poison. I. University of California Publications in Zoology, Vol. 41, No. 5.*

By W. Forest Whedon. University of California Press, Berkeley. 10½ x 6¾; 35–44; 1936 (paper).

NEW SPECIES OF SPIONIDAE (ANNELIDA POLYCHAETA) *from the Coast of California. University of California Publications in Zoology, Vol. 41, No. 6.*

By Olga Hartman. University of California Press, Berkeley. 10¼ x 6¾; 45–52; 1936 (paper).

SOME NEW AND LITTLE KNOWN AMPHIPODS OF CALIFORNIA. *University of California Publications in Zoology, Vol. 41, No. 7.*

By A. L. Alderman. University of California Press, Berkeley. 10¼ x 6¾; 53–74; 1936 (paper).

CROTALUS MITCHELLII, THE SPECKLED RATTLESNAKE. *Transactions of the San Diego Society of Natural History. Volume 8, Number 19.*

By Laurence M. Klauber. Society of Natural History, San Diego, Calif. 10⅛ x 6¾; 36; 1936.

NOTES ON BIRDS IN RELATION TO THE FAUNAL AREAS OF SOUTH-CENTRAL ARIZONA. *Transactions of the San Diego Society of Natural History, Volume 8, Number 18.*

By A. J. van Rossem. Society of Natural History, San Diego, Calif. 10⅛ x 6¾; 28; 1936.

BOTANY

THE MUSHROOM HANDBOOK.

By Louis C. C. Krieger. The Macmillan Co., New York. $3.50. 7½ x 5¼; xiv + 538 + 32 plates; 1936.

An excellent hand book which seems to be complete in every department. The novice will find it easily within his comprehension. After becoming thoroughly familiar with the section on mushrooms *safe for the beginner* he can confidently venture tackling the more difficult varieties. The section on poisonous mushrooms is so clear that one can scarcely fail to recognize these forms. The volume, however, is far more than a key to the mushroom family. Considerable space is given to conditions under which mushrooms grow and thrive, the habitats which the different varieties prefer, and the life history and general characteristics of mushrooms—even to bio-luminosity and monstrosities. The section on growing mushrooms artificially gives useful information to those wishing to venture into this field. The latter part of the book (pp. 181 to 454) is devoted to a systematic account of selected larger fungi with detailed descriptions of 238 types and a classification chart. There is also included in the volume some excellent recipes for cooking mushrooms, an index to the literature for identification of the larger fungi, a list of the principal authors of fungus species, a lengthy bibliography, a glossary and an index. The excellent illustrations—126 black and white drawings and photographs, and 32 colored plates from the author's paintings—add immeasurably to the value of the book.

J. ARTHUR HARRIS: *Botanist and Biometrician.*

Edited by C. Otto Rosendahl, Ross A. Gortner and George O. Burr. University of Minnesota Press, Minneapolis. $2.50. 9¼ x 6; viii + 209; 1936.

Dr. Harris (1880–1930) started his biological work with a paper on crayfish as an undergraduate at Kansas University, later taking his Ph.D. in botany at Washington University, St. Louis. He soon became interested in the mathematical approach to biological problems and after spending two winters in Karl Pearson's laboratory became a pioneer in introducing statistical methods into botanical problems.

Though the present volume is disappointing as a biography it contains the following previously unpublished papers of interest to workers in the fields represented: Some Chemical Factors of the Soil That Influences the Distribution of Desert Vegetation, by J. A. Harris and Vernon A. Young; The Distribution of Errors of Analyses, by J. A. Harris and Alan E. Treloar; The Length and Weight of the Newborn Infants of Various Nationalities, by J. A. Harris, Alan E. Treloar, and Borghild Gunstad; The Relationship Between Number of Pregnancies and Number of Births in Man, by J. A. Harris and Borghild Gunstad; The Measurement of the Individuality of Women with Respect to Their Capacity for Bringing the Foetus to Term, by J. A. Harris and Borghild Gunstad; Fecundity in the American-Born and Foreign-Born Inhabitants of New York City, by J. A. Harris and Borghild Gunstad; A Great Institute for the Study of the Psychology of the Mule, by J. A. Harris.

This last paper is a satire on the red tape in most government and university research departments.

MEDICAL MYCOLOGY. *Fungous Diseases of Men and Other Mammals.*

By Carroll W. Dodge. C. V. Mosby Co., Saint Louis. $10.00. 10 x 6¾; 900; 1935.

Many and varied are the types of fungous diseases of man, among them being such commonly known infections as dandruff, acne, ringworm, herpes eczema, etc.

This authoritative treatise is primarily a taxonomic reference work for the medical man. Introductory chapters cover general morphology and physiology of the fungi; the technique involved in culture media and the isolation of microorganisms; microscopy, and botanical nomenclature. The taxonomic data of the succeeding chapters are followed in the case of each group of microorganisms under consideration by a complete bibliography. This is the first time a bibliography so thoroughly covering this field has ever been available.

QUELQUES RÉSULTATS STATISTIQUES NOUVEAUX CONCERNANT LA FLORE VASCULAIRE DE QUÉBEC. *Contributions du Laboratoire de Botanique de l'Université de Montréal. No. 26.*

By Frère Marie-Victorin. Institut Botanique, Université de Montréal, Montréal. 15 cents. 9 x 6; 8; 1935 (paper).

This is a statistical study of the distribution of vascular plant species in the Province of Quebec. Of 142,600 known species 1917, or one and one-third per cent, have been found in this territory. This percentage has been estimated to be about the average for a unit of this area. The predominant families, *i.e.*, those with the most species represented, are the Cyperaceae, the Composites, and the Gramineae.

MORPHOLOGY OF VASCULAR PLANTS. *Lower Groups (Psilophytales to Filicales).*

By Arthur J. Eames. McGraw-Hill Book Co., New York. $4.00. 9 x 6; xviii + 433, 1936.

In this text book, the outgrowth of the author's experience in teaching, there is made available to the student the important changes in interpretation and classification of the morphology of vascular plants which recent studies have brought about. It is divided into two parts, the first dealing with the lower and the second with the higher groups. The view point is that of broad comparative study with the development of a natural classification and phylogenetic relationship as the goal. Emphasis is placed upon the range of structure within the group. Individual forms are not treated in detail, and cytological aspects have been largely omitted, as have many details of anatomical structure. Classification is built up as the groups are studied, and the goal of the study, a classification that is as closely natural as possible, is attained only at the end of the book. The living and fossil forms for most major groups are treated separately. Each chapter has a section devoted to discussion and summary and concludes with a bibliography. The volume is generously illustrated with excellent figures and photographic reproductions and contains a short general

bibliography and a detailed index. A sound and useful book.

BLACK ROCK FOREST PAPERS, *Vol. 1. No. 1, A Method for Determining the Nutrient Needs of Shade Trees with Special Reference to Phosphorus, by Harold L. Mitchell. No. 2, The Relative Feeding Power of Oaks and Maples for Soil Phosphorus, by H. L. Mitchell and R. F. Finn. No. 3, A Chestnut Oak Volume Table for the Hudson Highland Region, by H. H. Tryon and R. F. Finn. No. 4, The Effect of Varied Solar Radiation Upon the Growth, Development and Nutrient Content of White Pine Seedlings Grown Under Nursery Conditions, by H. L. Mitchell. No. 5, Differential Browsing by Deer on Plots Variously Fertilized, by H. L. Mitchell and N. W. Hosley.*

Black Rock Forest, Cornwall-on-the-Hudson, New York. 11 x 8½; 27; 1935–36 (paper).

MORPHOLOGY

NEUROEMBRYOLOGY. *An Experimental Study. By Samuel R. Detwiler. Macmillan Co., New York.* $3.75. 8½ x 5¾; x + 218; 1936.

This book, by one of the leading investigators in the field of neuroembryology, is designed "to discuss more specifically problems concerning the growth of peripheral nerves, factors influencing the proliferation of nerve cells, as well as the capacity of the developing nervous system to undergo structural and functional adaptations in response to new conditions experimentally imposed upon it." Experimental work of this nature has been largely upon *Amblystoma*, the frog and the chick. In the first 13 chapters of the book the author discusses the work of various investigators as well as his own important findings. From the final chapter on summary and interpretations, we give brief extracts:

. . . . experimental evidence is presented . . . . to show that in embryos from which the myotomes have been removed, so that the axial musculature is entirely wanting, motor nerve outgrowth is not suppressed. Only the segmental arrangement is destroyed.

The results of these and other experiments show that the brachial correlation mechanism is definitely limited within the cord and cannot be extended under experimental conditions.

. . . . experiments dealing with correlated limb function . . . . demonstrate that any spinal or cranial somatic motor nerves are capable of bringing about movements in grafted limbs. These movements, however, are always stereotyped and associated with those characterizing the region into which the limb has been grafted.

Evidence is presented to show that alteration in the number of sensory fibers entering the central nervous system influences cell division and differentiation in the centers penetrated by these fibers. When a peripheral sensory area such as the eye or nasal epithelium is ablated, or is augmented by grafting a supernumerary organ adjacent to the normal, the number of primary sensory neurons is changed.

. . . . local regions or peaks of accelerated proliferation within the brain wall influence the ingrowth of sensory nerve roots.

On the basis of the experimental results, a discussion is given of the causes of variations in the number of segmental nerves contributing to the limb plexus in different groups of vertebrates.

Experiments are also described in which reflex behavior is modified by the excision of certain coördinating projection tracts (Mauthner's fiber) present in fishes and aquatic amphibia. The cell bodies which develop these fibers lie in the medulla and their axones course through the entire length of the spinal cord.

A lengthy bibliography and an author and subject index are included in the volume.

A TEXTBOOK OF HISTOLOGY. *By Joseph Krafka, Jr. Williams and Wilkins Co., Baltimore.* $2.50. 9 x 6; vii + 246 + 1 plate; 1936.

This is a clearly-written and well-organized textbook of histology which attempts to picture, in not too great detail, the principal cellular features of human tissues and to relate these features with other fields of biology. The author is insistant that histology shall assume a position in modern biology comparable to that held by embryology, genetics, physiology, "evolution," biochemistry and comparative anatomy. He makes these points in an evangelistic fashion in the preface and obviously hopes that his book will do much towards placing histology on a more-appreciated plane. Whether this will be the case remains to be seen. In any event, the book will find users among the

group requiring an introduction to the facts of the subject even though they may not envisage the relation of microscopic anatomy to "diets," "public health," "popular medical education," "education," "criminology" and "social adjustment." The volume is indexed, but has no bibliography. The illustrations, which are mostly from pen and ink drawings, struck the reviewer as being of rather mediocre quality.

How Animals Develop.

By C. H. Waddington. W. W. Norton and Co., New York. $2.00. 8 x 5⅜; 128 + 7 plates; 1936.

This is a brief account of the science of embryology written for the "intelligent layman and the elementary student." Such features as fertilization and cleavage, germ-layer formation, organization centers of the embryo and the relation of these centers to embryonic pattern and differentiation, and later developmental specializations are discussed in the text. Unlike most books of this nature the author emphasizes the dynamic and experimental aspects of ontogeny and so imparts to his subject an interest which otherwise might be lacking. For example, he discusses such problems as vital staining and its bearing on an understanding of gastrulation; the "organizator" experiments of the Spemann group; the rôle of genes in development, etc. An excellent example of sound popularization of science.

Atlas of Human Anatomy *with Explanatory Text.*

By Jesse F. Williams. Colored illustrations by Franz Frohse, Max Brödel and Leon Schlossberg. Barnes and Noble, New York. $2.00. 8¼ x 5¼; 64; 1935.

The significant feature of this little atlas is the series of beautifully colored anatomical diagrams which cover twenty-five pages. As the book has an appeal to the inquiring layman as well as to the student of anatomy, the diagrams are labelled with the common names, followed by the Latin names in parenthesis. In the twenty-five initial pages of explanatory text, an effort is made to outline the workings of the anatomical systems, with frequent references to the accompanying diagrams.

The book is admirably suited to its purpose. However, it is not, and does not attempt to be, a textbook on anatomy. It is an accurate, beautiful, and comparatively complete little picture book of human anatomy.

Animal Micrology. *Practical Exercises in Zoölogical Micro-Technique.*

By Michael F. Guyer. With a chapter on drawing by Elizabeth A. (Smith) Bean. The University of Chicago Press, Chicago. $2.50. 8¾ x 6; xvi + 331; 1936.

The fourth edition of this popular text on histological technique (earlier noticed in Q.R.B., 1931: 6; p. 111) has been revised primarily by the introduction of a chapter (vii) on the dioxan method. By using dioxan, a liquid miscible both with melted paraffin and water, certain steps in the preparation of tissues, *e.g.*, absolute alcohol and xylol washings, may be omitted. This, according to the author, makes for a quicker and more simplified procedure and so justifies iself. Other minor changes and additions, too numerous to list, have been made throughout the text. The book's well-deserved success in the past will continue.

Six Conférences D'Histophysiologie Normale et Pathologique. *Substance Osseuse. Ossification Endochondrale. Alvéole Pulmonaire. Paroi Artérielle. Micro-incinération. Histospectrographie.*

By A. Policard. Masson et Cie, Paris. 15 francs. 9¾ x 6⅝; 105; 1935 (paper).

This book incorporates six lectures presented before the Medical Faculties of Buenos Aires in May, 1935. The subjects were: the formation of bone; the elementary processes of endochondral ossification; the alveolar membrane of the

lung and its histophysiological mechanisms; the arterial wall and some of its histophysiological mechanisms; the method of microincineration of cells and tissues; a new technique in histochemistry: histospectrography. The technique described in the last lecture was devised by the author and A. Morel in 1931 and 1932.

THE STUDY OF ANATOMY. *Written for the Medical Student. Third Edition, Revised and Enlarged.*

By S. E. Whitnall. William Wood and Co., Baltimore. $1.75. $7\frac{1}{4}$ x $4\frac{7}{8}$; viii + 113; 1936.

This useful little volume in its third edition (previously mentioned in Q. R. B., Vol. 9, No. 3) has been revised and enlarged. Its *raison d'être* is "to impress the medical student with the fact that human anatomy must be considered in relation to (a) the living body, (b) physiology and other cognate subjects, (c) future clinical work, and that dissection of the cadaver is only one way of studying it." A capital book.

LES MOUVEMENTS MORPHOGÉNÉTIQUES DANS LE DÉVELOPPEMENT DES VERTÉBRÉS. *Actualités Scientifiques et Industrielles, 303. Exposés de Biologie (Embryologie et Histogenèse), V.*

By Pierre Hatt. Hermann et Cie, Paris. 12 francs. 10 x $6\frac{1}{2}$; 57; 1935 (paper).

This number of the *Actualités* presents a brief résumé of present knowledge concerning the morphogenetic processes in the early embryological stages of batrachians and birds. Three pages of detailed comparison between the first steps in the morphogenesis of birds and that of batrachians are included. There is a bibliography.

PHYSIOLOGY AND PATHOLOGY

THE PATIENT AND THE WEATHER. *Volume 1, Part 2, Autonomic Integration.*

By William F. Petersen and Margaret E. Milliken. Edwards Bros., Ann Arbor, Mich. $9.00. $10\frac{3}{4}$ x $8\frac{1}{4}$; xxx + 781 + 2 folding charts; 1936.

In this second part of Vol. 1 (other volumes have been reviewed previously in this journal), the author presents evidence to show the association between changes in the atmosphere and modifications of individual physiologic reactions. In a first chapter he discusses asthenics and pyknics and the different morbidity found associated with the two physical types. The following chapters discuss meteorology and meteoropathology. Then the author presents the detailed study of four "normal" subjects: The influence of meteorologic changes on their metabolic activity, blood picture, blood pressure, temperature, weight, N. P. N. and other physical and psychic conditions. There are other chapters in which the author indicates the effect of weather changes on pregnant women, children, and individuals suffering from specific infections. All these and other facts led the author to conclude "that the organism adjusts to the meteorological environment by the three major components of the autonomic apparatus—chemical, endocrine, nervous." And, "the organism swings in a definite rhythm of increasing and decreasing oxidation, of increasing and decreasing pH, of increasing and decreasing metabolism, of increasing blood pressure, all clearly inter-related to the meteorologic environment." Finally, "while the organism seeks to maintain a proper balance by such a rhythm in the normal biological processes, the peaks and troughs are of clinical significance because here lack of prompt integration frequently leads to dysfunction, to disease, and finally to death."

The cases presented are excellent illustrations of this beautiful theory; however, as was remarked in our other reviews, the author fails to give the statistical evidence to support the theory. It is doubtful whether such evidence will ever be forthcoming from the author since in the preface he classifies it as a "scientific superstition" to believe "that a series of observations made at random, when compiled and leveled, have more signifi-

cance than the carefully controlled individual observation."

This is the most important volume of the series and deserves a careful study. The extensive bibliography will be found useful.

BODY WATER. *The Exchange of Fluids in Man.*

By John P. Peters. Charles C Thomas, Springfield, Ill. $4.00 postpaid. 9 x 6; ix + 405; 1935.

An important treatise. In the preface the author says: "For many years the author with his associates has been engaged in studies of the distribution and movements of solutes and water in the human body. The experiments have involved such diverse fields of pathology and physiology that they may seem planless. The work has inevitably followed an opportunist course, turning to any clinical condition which promised however remotely to provide favorable experimental material and often enough abandoning the clinic entirely for the normal subject or the test tube." Nevertheless there have been certain definite guiding motives. Chief of these has been "the desire to test certain plausible hypotheses concerning the nature of restraints imposed by vital membranes in the body upon movements of fluid and electrolytes, and the influence which they have in the production of various clinical and pathological disturbances."

The work has been entirely restricted to the human subject and the present treatise represents a summary or survey of the whole field of the investigations in order to estimate the value of the original working hypothesis, to find gaps in the investigations, to perceive new points of experimental approach, and to attempt to construct a background for a more rational analysis of the functional pathology of renal disease. In order that the reader may obtain a general idea of the scope of the work we give the chapter headings: Chemical forces which control exchanges of fluid and solutes; the nature and movements of interstitial fluid and lymph; exchanges between blood and interstitial fluids; serous fluids and transudates; exchanges between blood cells and serum; exchanges between tissue cells and interstitial fluids; water of oxidation and the losses of water and solutes through skin and respiratory passages; alimentary exchanges; the general nature of renal activity; renal excretion of filtrable organic solutes; renal excretion of water and inorganic salts; nervous and hormonal control of urine excretion.

In the bibliography and author index there are 875 titles.

THE ADRENALS.

By Arthur Grollman. The Williams and Wilkins Co., Baltimore. $5.00. 9 x 6; xii + 410; 1936.

According to the preface, an attempt has been made in the present volume, ". . . . to analyze the great accumulation of literature on the subject of the adrenals and present a working hypothesis from which the reader may start on his own efforts." The text material is divided into the following major divisions: Part I, "Anatomical Considerations"; Part II, "The Medulla"; Part III, "The Cortex," and Part IV, "Clinical Considerations." In the first part the gross and microscopic anatomy of the adrenals, as well as the morphology of the androgenic tissue (a portion of the adrenal which in certain pathological conditions gives rise to reproductive disorders) is discussed. Part II deals principally with the chemistry and pharmacology of epinephrine and the physiology of the medulla. Part III discusses such topics as the relation of the adrenal cortex to the general endocrine system; specific functions of the cortical hormone; the adrenals and metabolism, etc. The final part considers Addison's disease, adrenal tumors, the "adrenogenital syndrome" and other diseases of this gland.

This book is a competent review of many of the pertinent data about the adrenal glands and houses within its covers a wealth of carefully concentrated information presented in a logical fashion. It is certain that the volume will find a

warm welcome among endocrinologists. An excellent bibliography, adequate index and interesting historical summary of the field supplement the text.

NEW FACES—NEW FUTURES. *Rebuilding Character with Plastic Surgery.*

By Maxwell Maltz. Richard R. Smith, New York. $3.00. 8½ x 5½; xv + 315; 1936.

The history of plastic surgery is a vivid one: it is strewn alike with charlatans and remarkably skillful surgeons. Unfortunately, the former are still with us. Fortunately, the latter are multiplying and along with their multiplication has come new technical skills. It is with the latter group and their achievements that this book concerns itself and, because of the human interest of the subject, it can be recommended as interesting reading. Using "before and after" pictures to supplement the text the author discusses some of the operations common to modern plastic surgery (*e.g.*, hare-lip reconstruction, nose straightening, blemish removal, etc.) and shows how many of them have a favorable prognosis in respect of pulchritude as well as health and psychical well-being. The latter point is an interesting one. Apparently, the plastic surgeon frequently corrects unhappy mental disturbances traceable to prominent disfigurements when he improves the physical appearance of the patient. Many of the chapters are headed with such titles as, "Mr. Gump and Dick Tracy," "The knight of the silver nose," "A new deal for Cyrano," "Wrinkles, those damned democrats, won't flatter," etc. Did anyone beyond a mental age of six ever think this sort of thing was funny?

EVANS' RECENT ADVANCES IN PHYSIOLOGY. *Fifth Edition.*

Revised by W. H. Newton. P. Blakiston's Son and Co., Philadelphia. $5.00. 7⅞ x 5¼; xii + 500; 1936.

Some notion as to the revisions made in the present edition (fifth) of this book can be obtained from the following statement by the present reviser:

> Time may add charm to a work of art, and dignity even to a scientific textbook, but it deals harshly, almost vindictively with a work pretending to the title of "Recent Advances." This is nowhere more apparent than in the present volume, from which the unremitting pressure of new research has displaced several masterpieces of exposition. Only Chapters I, III, and VIII (coronary circulation; carotid sinus as a regulator of circulation; nerve conduction) have been carried over from the last edition, and even these have been greatly altered to bring them up to date, and they contain many new sections. The remaining eight chapters (cardiac muscle metabolism; carbonic anhydrase; foetal oxygen supply; sex hormones; chemical transmission at nerve endings; spinal reflex; urine secretion; nervous control of micturation) are quite new. . . .

It would be superfluous to say this is a good book. The fact that the volume has been through five editions since 1925 and that it has been enthusiastically reviewed on two occasions in this journal (Q. R. B., 1926: 1: p. 458 and 1927: 2: p. 461) amply attest the point.

SÉROTHÉRAPIE ANTIPOLIOMYÉLITIQUE D'ORIGINE ANIMALE (S.A.P.) *Seize Années d'Expérimentation Clinique.*

By Auguste Pettit. Masson et Cie, Paris. 30 francs. 10 x 6½; 271; 1936 (paper).

Pettit's horse serum has been used clinically in the treatment of poliomyelitis more extensively than any other horse serum. His experiments with this serum, begun in 1917, have continued to the present time. In 1929 he succeeded in preparing an immune serum from *Cynocephalus* and in 1932 successfully immunized a chimpanzee. The first part (56 pages) of this book describes the methods employed in the production of the immune sera from these animals.

The second part of the book is devoted largerly to case histories from the files of physicians (with few exceptions French) who have used the Pettit serum in their practice. On the basis of these Pettit claims that among its attributes are (1) that with the injection of the serum in the preparalytic stage, subsequent paralysis and paresis do not occur; (2) that it blocks the infection and combats the ascent of

the virus; (3) that it diminishes the gravity of the sequelae when it does not suppress them entirely; and (4) it reduces the mortality from this disease by about one half. Some untreated cases are tabulated in comparison with treated cases but the numbers seem to us too small to test the efficaciousness of the serum. As the value of immune serum in the treatment of infantile paralysis is still a matter of debate it is to be regretted that more control cases were not included. However, as the stages of the disease at treatment and the route of administration of the serum are noted, it is well to have these cases on record.

A feature of the 28-page bibliography is the inclusion of abstracts of many of the items, and notes replying to criticisms or erroneous statements concerning the author's work.

OCCUPATION AND HEALTH. *Encyclopaedia of Hygiene, Pathology and Social Welfare. Vol. I, A-H; Vol. II, I-Z.*

International Labor Office, Geneva. U. S. Agents: World Peace Foundation, 40 Mt. Vernon St., Boston. £4; $22 (paper). $24 (cloth). $10\frac{7}{8}$ x $7\frac{1}{4}$; Volume 1, xxvi + 999; Volume 2, vii + 1310; 1930 and 1934.

The Health Section of the International Labour Office in Geneva has compiled this encyclopedia of Industrial Hygiene for the purpose of bringing together all the information available on the relation between working conditions and the health of the workers. The topics are listed in alphabetical order and the articles regard occupations, manufactured products, body organs, chemicals, diseases, etc. Some of the articles have been written by members of the staff of the Health Office, others are the contributions of medical specialists. All articles, in general, follow a definite pattern and contain descriptions of the industrial processes, the causes of disease, symptoms and diagnosis of the disease, statistical data on morbidity and mortality, comparative legislature enacted for the worker's benefit, and bibliography. As is to be expected, some articles are better written and more complete than others. This is due to a number of factors, but principally because there is more information available for some topics than for others. The bibliography is generally limited to textbooks and general reference books. One criticism that must be made is that in some cases the findings of an author are quoted without giving any information on the whereabouts of the original report. The physician and human biologist will find these volumes useful.

ELEMENTARY HUMAN PHYSIOLOGY.

By Sherburne F. Cook. Harper and Bros., New York. $3.50. $8\frac{1}{2}$ x $5\frac{3}{4}$; xi + 539 + 2 plates; 1936.

LABORATORY MANUAL IN ELEMENTARY HUMAN PHYSIOLOGY.

By Sherburne F. Cook and Mary A. Burmester. Harper and Bros., New York. $.50. $8\frac{1}{2}$ x $5\frac{1}{2}$; iii + 76; 1935 (paper).

The textbook is up to date and quite comprehensive. What is perhaps even more important, it is so well written that many students will read assignments in it! Unfortunately, there is no bibliography whatsoever and not a reference to help a student follow up a topic that interests him. Also the author, doubtless unwittingly, gives the impression that he has said the last work on every subject covered. Even elementary students will instantly recognize how improbable this is.

The laboratory manual is a paper bound pamphlet giving detailed instructions for a rather well planned series of experiments. Leading questions are asked about each experiment.

GRUNDLAGEN DER EPIDEMIOLOGIE.

By Georg Jürgens. Johann Ambrosius Barth, Leipzig. RM 7.50. $9\frac{1}{4}$ x $6\frac{1}{4}$; ix + 165; 1936 (paper).

This little book divides into four parts. Part I is a discussion of the fundamental principles of infectious diseases, and deals with such subjects as the mechanisms of infection, the incubation period, and

immunity. In Part II the author gives a few partly historical researches on epidemiology. He discusses here the importance of epidemics in public health, and epidemic and endemic infections. Part III is devoted to the origin and spread of an epidemic, the interrelations of epidemics to each other, and the importance of a condition of immunity. In Part IV a section is devoted to the use and misuse of statistics.

A Handbook of Urology for Students and Practitioners.

By Vernon Pennell. University Press, Cambridge; Macmillan Co., New York. $2.75. 7¼ x 5; viii + 224; 1936.

This book by a well known English surgeon has been designed to place before the many students and practitioners who have not had post-graduate instructions in this field a short and concise account of urinary diseases, with their method of investigation and treatment. Rare diseases and uncommon and obsolete treatments have been rigorously pruned, and venereal diseases and other infections of the genital tract have been largely omitted. Only those methods now most commonly employed in operating are described. In an appendix is given a list of drugs and preparations for use in urological cases. The volume is illustrated and indexed.

A La Recherche du Temps Vécu. *Actualités Scientifiques et Industrielles, 288. Exposés de Physiologie, VIII.*

By R. S. Lacape. Hermann et Cie, Paris. 12 francs. 10 x 6½; 55; 1935 (paper).

Time as measured by physical instruments does not always correspond to the "time lived" by the living organism. Therefore, in order to understand and study the succession of events that occur in the living organism it is necessary to find a measure of "physiological" time which is independent of "physical" time. And, since the concept of time is a product of the mind, the mechanism which measures it must be sought for in the brain. This is the essence of the author's thesis which is founded on Bergsonian philosophy. The discussion is in the main theoretical, savours of the metaphysical, and is not easily understandable to the empiricist.

Autres Scenes de la Vie Animale. *Voyage en Amérique de Sud. Quatrième édition.*

By Léon Binet. Gallimard, Paris. 12 francs. 7½ x 4½; 143; 1935 (paper).

This little book, written by an eminent physiologist, is the elaboration of some notes jotted down on a lecture tour to Argentina and Uruguay. It contains short sketches of some of the aquatic, reptilian, mammalian and avian life of these countries but is concerned rather with physiological implications than natural history. It is interestingly written. Bibliographies are appended to each of the chapters.

Les Parathyroïdes. *Actualités Scientifiques et Industrielles, 307. Histophysiologie, I.*

By Harald Okkels. Hermann et Cie, Paris. 10 francs. 10 x 6½; 26; 1935 (paper).

This volume starts a new sub-series of the *Actualités*, under the title *Histophysiologie*, edited by Professor Policard. The author clearly outlines what is known about the parathyroids and their influence on the muscular, nervous and bony systems of the body; their morphology, biochemistry, physiology, and pathology; and discusses preparations containing parathyroid hormones and their standardization.

La Secretion de L'Adrenaline son Mécanisme Neuro-Humoral. *Actualités Scientifiques et Industrielles, 273. Exposés de Physiologie, VI.*

By B. Minz. Hermann et Cie, Paris. 12 francs. 10 x 6½; 47; 1935 (paper).

The author has very ably brought together in a small space the results of a large body of material dealing with the secretion of adrenalin. In many cases no attempt is

made towards definite conclusions and controverted opinions are given as such. Although some American workers are included in the four-page bibliography, the greater part is devoted to French, German and English researches.

CHINESE MEDICAL JOURNAL SUPPLEMENT *No. 1. Pathology and Microbiology. Being Mainly Proceedings of the Chinese Society of Pathology and Microbiology held in Canton, November 5–8, 1935.*

Chinese Medical Journal, Peiping. $2.50. 10 x 7; 518 + 75 plates; 1936 (paper).

This first number of the Supplement Series—of the same size and format as the regular issues of the Chinese Medical Journal—has brought together a number of papers on pathology and microbiology. There is also an excellent article on *Methods of Illustrating Scientific Papers.* All of the papers are in English.

ALTERS-FORSCHUNG. *Untersuchungen und Berichte über Lebensdauer, Altern und Tod. 2 Jahrgang.*

Edited by Josef Kluger. Josef Kluger, Gartenstrasse 135, Wünschelburg-Heuscheuer. 3 marks. 9¼ x 6⅝; 40; 1936 (paper).

The second volume of this annual devoted to the investigation of senescence and senility contains a brief and rather vague summary of some recent studies on longevity and how to keep from growing old. The last half of the pamphlet, and by far the most useful, is a bibliography of anything concerning longevity that has appeared in the last two years and has come to the editor's attention.

REPORT OF THE PAN-AFRICAN HEALTH CONFERENCE HELD AT JOHANNESBURG, NOVEMBER 20TH TO 30TH, 1935. *League of Nations. Quarterly Bulletin of the Health Organisation. Vol. 5, No. 1.*

League of Nations. League of Nations, Geneva: World Peace Foundation, New York. 65 cents. 9½ x 6⅝; 209; 1936 (paper).

BIOCHEMISTRY

ALCALOÏDES (*Première Partie*). (*Généralités, Ptomaines et Leucomaïnes. Drogues a Alcaloïdes Liquides Toxiques. Opium et ses Alcaloïdes*). *Actualités Scientifiques et Industrielles, 262. Leçons de Toxicologie VII.*

By René Fabre. Hermann et Cie, Paris. 12 francs. 10 x 6½; 65; 1935 (paper).

ALCALOÏDES (*Deuxième Partie*). (*Des Solanées Mydriatiques, de la Coca, des Aconits, des Strychnées, Liliacées. Genalcaloïdes*). *Actualités Scientifiques et Industrielles, 263. Leçons de Toxicologie VIII.*

By René Fabre. Hermann et Cie, Paris. 12 francs. 10 x 6½; 59; 1935 (paper).

TOXIQUES MINÉRAUX (*Première Partie*). *Généralités. Arsenic, Antimoine. Actualités Scientifiques et Industrielles, 292. Leçons de Toxicologie, IX.*

By René Fabre. Hermann et Cie, Paris. 12 francs. 10 x 6½; 69; 1935 (paper).

TOXIQUES MINÉRAUX (*Deuxième Partie*). *Mercure. Bismuth. Plomb. Thallium. Actualités Scientifiques et Industrielles, 293. Leçons de Toxicologie, X.*

By René Fabre. Hermann et Cie, Paris. 12 francs. 10 x 6½; 57; 1935 (paper).

TOXIQUES MINÉRAUX (*Troisième Partie*). *Cuivre. Zinc. Chrome. Nickel. Manganèse. Baryum. Radium. Métalloïdes Divers. Actualités Scientifiques et Industrielles, 294. Leçons de Toxicologie, XI.*

By René Fabre. Hermann et Cie, Paris. 15 francs. 10 x 6½; 69; 1935 (paper).

This textbook of medicolegal toxicology deals primarily with the relative usefulness of various means of detecting the presence of poisons in human cadavers, principally: alkaloids (to which 120 pages are devoted) arsenic, antimony, mercury, bismuth, lead, thallium, copper, zinc, chromium, nickel, manganese, barium, and radium. For the purposes of the lecture room the treatment is quite satisfactory; the merits and demerits of the commonly employed chemical tests are nicely balanced, and there is a great deal of sound advice intended to keep an ambitious young toxicologist from making a fool of himself in court. It pains us to observe, however,

that a book as interestingly written as this should entirely lack bibliographic citations and an index. Also the author is inclined to be a bit vague about the practical details of laboratory work.

LES SOLUTIONS CONCENTRÉES. *Théorie et Applications aux Mélanges Binaires de Composés Organiques.*

By Jean Timmermans. Masson et Cie, Paris. 130 francs. $9\frac{3}{4}$ x $6\frac{1}{2}$; 646; 1936 (paper).

This is an extremely thorough treatise limited to binary solutions of organic compounds in which the two components are present in comparable quantities. It is further restricted by the exclusion of all systems for which there are no data between 10 and 90 gm. per cent, or only one datum between 10–20 gm. per cent or 80–90 gm. per cent, but even so this is a weighty tome. The book is divided into three parts. Part I deals with systems in which there is an analogy of structure between the components; Part II, with components of different chemical types; and Part III with systems in which one of the components includes a hydroxyl group. Each chapter, furthermore, consists of two parts: (1) a clear theoretical discussion with the more abstract points clearly explained by examples; and (2) a series of diagrams (540 in all), many of which include more than one property in the same figure, and lists of solutions, their properties, and discoverers. The author has provided a twenty-six page bibliography and an index of formulae, arranged in the sequence used in Richter's *Lexicon*, beginning with methane, CH_4 and ending with tristearine, $C_{57}H_{110}O_6$. The thoroughness with which this book has been prepared may be noted by an example: reactions for benzene are mentioned in over 300 combinations. Timmermans has rendered a great service to his colleagues in preparing this book.

ANNUAL REVIEW OF BIOCHEMISTRY. *Volume V.*

Edited by James M. Luck. Annual Review of Biochemistry, Stanford University P.O., Calif. $5.00. $8\frac{3}{4}$ x 6; ix + 640; 1936.

The *Annual* is becoming increasingly important to workers in biochemistry. The present volume follows the same general plan of previous volumes and maintains the same high standard. As is customary the authors of the sections differ from time to time, as well as the arrangement of the subject matter. In this issue there has been added a section on X-ray studies on the structure of compounds of biochemical interest. The authors, O. L. Sponsler and W. H. Dore point out that a "complete knowledge of the structure of a given biochemical substance should afford valuable information as to its molecular stereochemistry and should play an important rôle in the solution of such vexing problems as the mechanism of optical rotation and the existence of various ring types among the sugars."

We also note that the vitamins are now treated under two headings. H. von Euler writes on the water-soluble vitamins and E. V. McCollum on the fat-soluble vitamins.

To the student the excellent literature lists accompanying the chapters are invaluable. The volume has an index of author's names but no general index.

MANUEL DE BIOCHIMIE.

By Pierre Thomas. Masson et Cie, Paris. 180 francs. 10 x $6\frac{1}{2}$; vi + 978; 1936.

This book has been prepared for the use of physicians and biologists who for lack of time have not been able to keep abreast of the advances in biochemistry as published in the large number of technical treatises and journals not devoted to their own field. The author has here brought together a large body of literature and produced an up-to-date manual (to the end of 1935). Directions are included for the latest methods of the preparation and determination of dosages, reactions, and extractions. A table of "practical exercises" and an index are appended.

EXPERIMENTAL ENZYME CHEMISTRY.
By Henry Tauber. Burgess Publishing Co., Minneapolis. $3.50. 10¾ x 8½; v + 118; 1936.

A mimeographed text, confining itself to the more important of recent researches, and generally eschewing theoretical considerations in order more directly to concentrate upon the experimental aspects of enzyme chemistry. It carries extensive recent bibliographies following each of its eleven chapters. The book is really an admirably condensed review of recent literature, with running directions for laboratory work included in the text. The general biologist will find it useful to have at hand.

TRAITÉ DE CHIMIE ORGANIQUE. *Tome II. Fascicule I et II. Propriétés Optiques des Combinaisons Organiques. Structure des Molécules et Spectres d'Absorption. Spectres de Fluorescence. Application des Rayons X à l'Etude des Composés Organiques. Effet Raman. Propriétés Diélectriques et Constitution Chimique. Propriétés Magnétiques et Constitution Chimique. Parachor et Constitution Chimique. Mécanisme des Réactions. Radicaux Libres Organiques. Transpositions Intramoléculaires. Empêchement Stérique. Catalyse. Antioxygènes et Prooxygènes*, by P. Ramart-Lucas, A. Andant, M. Auméras, H. Bonnet, M. Bourguel, E. Carrière, E. Darmois, C. Dufraisse, A. Kirrmann, J. Lecomte, J. Martinet, C. Mauguin, P. Pascal, L. Piaux, G. Vavon.
Published under the direction of V. Grignard and Paul Baud. Masson et Cie, Paris. 280 francs. 10 x 6½; xv + 1273; 1936.

This is the third volume to appear of a comprehensive *opus* on organic chemistry ultimately to comprise fifteen volumes. Volumes I and III have already been noticed in these columns in Numbers 1 and 3, respectively, of the current volume. The scope of the two parts noticed here is sufficiently indicated in the subtitle.

ESSAI SUR LA BIOCHIMIE GÉNÉRALE ET COMPARÉE DES PIGMENTS RESPIRATOIRES.
By Jean Roche. Masson et Cie, Paris. 40 francs. 10 x 6½; 170; no date (paper).

This monograph on the respiratory pigments is approached from the point of view of correlating chemical structure and physiological effect. It is clearly and succinctly written and is addressed not only to specialists but to all those interested in biological problems. An appendix describes methods of preparation for study and methods of measurements. A bibliography of 17 pages is included.

LES PARENTÉS CHIMIQUES DES ÊTRES VIVANTS. *Actualités Scientifiques et Industrielles, 282. Exposés de Physiologie, VII.*
By Paule Lelu. Hermann et Cie, Paris. 10 francs. 10 x 6½; 47; 1935 (paper).

This is a review of the numerous investigations regarding the comparative biochemistry of the different classes of animals. The author discusses briefly but adequately the work of Needham, Arnold and Luck, Clementi and others. He summarizes their results and seeks to demonstrate that certain chemical affinities between different species can be used as a criterion to establish their position in the evolutionary scale.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 451. Fermentforschung.* Containing following articles: *Pektinfermente (Pektinasen)*, by Felix Ehrlich; *Die Isolierung von kristallisiertem Trypsinogen und dessen Umwandlung in kristallisiertes Trypsin*, by M. Kunitz and J. H. Northrop; *Amylase (Nachtrag)*, by Theodor Sabalitschka; *Vereinfachung der Methodik des Nachweises von Abwehrproteinasewirkungen (Nachtrag)*, by Emil Abderhalden.
Urban und Schwarzenberg, Berlin. 13 marks. 10 x 7; 206; 1936 (paper).

SEX

MEDICAL HISTORY OF CONTRACEPTION. *Medical Aspects of Human Fertility Series Issued by The National Committee on Maternal Health, Inc.*

By Norman E. Himes. The Williams & Wilkins Co., Baltimore. $7.00. 9¼ x 6½; xxxi + 521; 1936.

Dr. Norman Himes has put all students of human biology much in his debt by the production of this substantial treatise. Most students of population problems, including Dr. Himes, adhere to the view that the practice of contraception is virtually the sole causal factor of importance concerned in the widespread decline of human birth rate in the last half century or so. There are still a few hardy souls, of whom the late John Brownlee and Udny Yule in England are notable examples, who have thought the matter less simple than this. But it is obvious that under the circumstances, there is need for a systematic examination of the history of man's ideas and behavior about tampering with the normal functioning of his reproductive mechanisms, to the end that he may enjoy his sexual cake without having to pay for it, as it were. Such a history, carefully wrought, Dr. Himes now provides.

The book starts with ethnological evidence from preliterate societies, goes on to the peoples of antiquity in the western world (Egyptians, Greeks, Romans, and biblical folk), and then to eastern cultures (China, Japan, and India). The next section of the book discusses contraceptive techniques in Europe during the Middle Ages and early modern times. In this section is included a long history of the condom, of which some 317 million are said to be manufactured in the United States annually.

The remainder of the book traces the history of the birth control movement during the 19th century in Europe and America, and an examination of the procedures and statistical results of birth control clinics.

The documentation is extensive, the bibliography covering some 60 pages of 8-point type. Detailed author and subject indexes round out a valuable and useful work.

FRIENDSHIP-LOVE IN ADOLESCENCE. *By N. M. Iovetz-Tereshchenko. George Allen and Unwin, London.* 16s. 8½ x 5½; xvi + 367; 1936.

Friendship-love is defined by the author as a mental state of a sublime nature experienced towards a person or group of persons of the same or opposite sex. In contrast, the author believes that a mental state is sexual if it is provoked or directed towards a person of the opposite sex, if reproduction is its purpose, or it is associated with "venereal voluptuousness" or physiologic activity of the sex organs. Having defined (*sic*) his terms, he attempts to prove that in childhood there can exist only friendship-love untainted by the sexual. The evidence to support his thesis is given by the diary of a Russian school boy compiled from the thirteenth to the sixteenth year of age. The diary describes the child's friendship and affection for other boys and girls, his jealousy, and all the other manifestations of the sensitive adolescent mind. Since apparently none of the sensations experienced by the writer of the diary can be classified as sexual, the author concludes that love is entirely independent of the sexual. Aside from the fact that this theory has been the favorite subject of the more idealist philosophers and romantic poets, the evidence presented by the author does not prove his thesis unless it is shown that the writer of the diary set down in it *all* the sensations he experienced. This is doubtful. For example, the author states that the diarist, now an adult, recalls the unique sensation of his first nocturnal emission, yet it is not mentioned in the diary. In fact, from a careful perusal of the diary, it seems the product of a school boy imitating the style of romantic prose writers. Nevertheless it is an interesting document and would be more effective if the author had translated it into literary English instead of attempting a literal translation, even to the point of presenting in English the equivalents of the child's Russian abbreviations.

DÉTERMINISME ET RÉALISATION DANS LE DEVENIR DU SEXE. *Actualités Scientifiques et Industrielles, 300. Exposés de Biologie*

(*La Cellule Germinale dans l'Ontogénèse et l'Évolution*), *V*.

By Vera Dantchakoff. Hermann et Cie, Paris. 18 francs. 10 x 6½; 74; 1935.

In the light of recent experiments on the reversal of sex, this characteristic can no longer be explained as solely due to the genetic constitution of the germ cells or to the balance of sex chromosomes and autosomes. In view of this the author attempts to summarize all the facts on the subject, and from this summary derives the following general proposition on sex determination. The constitution of the germ cell, the decisive agent for the realization of sex, permits a double orientation since it contains both male and female elements. Therefore, the genetic sex characteristics can be realized only when a specific and particular relationship is established between the germ cell and the environmental tissues. In other words, sex is a resultant of genetic and environmental (somatic) factors either of which can be modified.

There is actually nothing new in these statements. However they deserve to be emphasized especially for the benefit of some writers of current textbooks on genetics. The exposition of the author is, as usual, clear and her analysis is well corroborated by facts drawn from her own experimental work and that of others.

FRIGIDITY IN WOMEN. *Its Characteristics and Treatment.*

By Eduard Hitschmann and Edmund Bergler. Translated by Polly L. Weil. Nervous and Mental Disease Publishing Co., Washington. $2.00. 9 x 6; v + 76; 1936.

In this monograph the authors reiterate the classical Freudian theory regarding the influence of subconscious repressions on sexual behaviour. They classify the causes of frigidity in women into 18 groups, beginning with the Oedipus complex and ending with constitution. Illustrative examples are given and the prognosis for each type of frigidity is discussed. Two typical cases supposedly cured by psycho-analysis are described fully and at length.

BIOMETRY

GRAPHS. *How to Make and Use Them.*

By Herbert Arkin and Raymond R. Colton. Harper and Bros., New York. $3.00. 9⅛ x 6⅛; xvi + 224 + 1 plate; 1936.

In 1915 a committee of the American Statistical Association attempted to standardize certain procedures related to graphs and graphing. This committee, however, emphasized primarily the theoretical principles involved in making graphs and did not discuss to any extent the technique of construction of the graphs themselves. During the last two decades, although graphs have been used more and more extensively, little attempt has been made to crystallize standards of perfection towards which all authors should strive. The writers of the present volume have attempted to set up these standards and obviously hope that they will be adopted. Whether this will be so seems rather dubious at the moment, since most people have a tendency to continue using the types of graph with which they are familiar regardless of their value or soundness. But in any case this book does give a wealth of practical, understandable material about the usual graphic forms with examples of their adaptability to specific data and suggestions as to their construction. The biologist will find some of the material of little direct use, especially the generous discussions of methods applicable only to business and advertising purposes. Even so, the book is a commendable one and should find supporters among the biometricians as well as other folk interested in picturing quantitative facts.

AN OUTLINE OF BIOMETRIC ANALYSIS.

By Alan E. Treloar. Burgess Publishing Co., Minneapolis. $3.10. 10¾ x 8½; [6] + 193; 1936.

This textbook of statistics has for its purpose to acquaint the student of biometry with the principles underlying some of the more complex forms of analysis. The first part of the book contains a brief introduction to the history of statistics and is followed by a description of the fundamental formulae for the calculation of constants in the case of univariate and

bivariate frequency distributions. Parts 2 and 3 treat of correlational analysis and statistical estimation, including the methods proposed by R. A. Fisher. There is an appendix with some useful tables.

This is without doubt one of the best of the recent textbooks on statistics because the author always states clearly what are the theoretical foundations on which a formula rests. As a result, the student is enabled to realize the limits of applicability of a particular method of analysis. This is sufficient merit to recommend the book as supplementary reading for students of biometry.

METHODS OF STATISTICAL ANALYSIS.

By C. H. Goulden. Burgess Publishing Co., Minneapolis. $3.00. 10¾ x 8½; ii + 165; 1936.

The main purpose of this book is to illustrate the applications of R. A. Fisher's methods of analysis. The first two chapters are concerned with elementary statistics: frequency tables, calculation of the mean, the standard deviation, and the constants of a normal curve. The author then proceeds to discuss and give numerous examples of the computations involved in the tests of significance, correlation coefficients, regression, analysis of variance and of covariance, etc.

This book will be found useful by the student already well-grounded in statistics and interested in learning the mechanics of applying the formulae in question. It cannot be recommended for the beginner because the treatment of elementary statistics is too sketchy, the elements of the theory of probabilities have been omitted, and no attempt has been made to elucidate the theoretical foundations and limitations of the formulae discussed.

MÉTHODES STATISTIQUES APPLIQUÉES À LA PATHOLOGIE VÉGÉTALE.

By J. Dufrenoy. Annales des Epiphyties et de Phytogénétique 1: 147–256 1934–1935 (1936).

There has existed for sometime a need for a comprehensive treatise on the applications of statistical methods to special fields in plant pathology. Dufrenoy has bridged the gap between the studies of biometricians and the results of the present day investigators in the special field mentioned. Of particular interest are the sections dealing with the reliability of results of the application of fungicides to crop plants under field conditions; with the "causes" which are admittedly complex. Especially good is the emphasis on the way in which the study of distributions permit one to represent the effects of pathological agents. There is a good bibliography and the paper is well indexed.

BEITRÄGE ZUR DEUTSCHEN STATISTIK. *Festgabe für Franz Žižek zur 60. Wiederkehr seines Geburtstages.*

Paul Flaskämper and Adolf Blind, Editors. Contributions by Blind, Burkhardt, Flaskämper, Gerloff, Grävell, Hecht, Henzel, Jörges, Lind, Lüer, Meyer, Morgenroth, Müller, Schäfer, Seutemann, Vershofen, Winkler and Zahn. Hans Buske, Leipzig. 9 marks. 9 x 6¼; viii + 288; 1936 (paper).

A collection of papers published by students of Professor Žižek in honor of his sixtieth birthday. The contents are arranged under the following heads: General problems of German statistics (four papers): statistical theory (three papers); the organization of statistical boards (two papers); and population and economic statistics (nine papers).

PSYCHOLOGY AND BEHAVIOR

PHYSIQUE AND PSYCHOSIS. *An Analysis of the Postulated Relationship between Bodily Constitution and Mental Disease Syndrome. Comparative Psychology Monographs Vol. 13, No. 1, Serial No. 61.*

By Edward M. L. Burchard. Johns Hopkins Press, Baltimore. $1.25. 10 x 7; 73; 1936 (paper).

This monograph treats of the relationship between somatic characteristics and types of psychoses. In the first part, the author reviews, rather superficially, the extensive

literature which has followed Kretschmer's original publication. He concludes that most of the reports, including Kretschmer's, are subject to criticism from several standpoints and that therefore Kretschmer's hypothesis has yet to be definitely proven or disproven.

The remaining sections of this book contain a description of the author's investigation on 407 male white hospital patients. These include 125 schizophrenics and 125 circulars; the rest constitute a control group. When the patients are classified according to body type it is evident that there exists a positive association between pyknic habitus and circular insanity, and between asthenic habitus and schizophrenia. However, from group comparisons of certain anthropometric measurements and indexes, the author notes that "although significant anthropometric differences appear between the two psychoses, the amount of overlapping is so great that such differences are of very slight or no diagnostic value." As the author well realizes the analysis is incomplete and the results far from novel.

EFFECTIVENESS OF TOKEN-REWARDS FOR CHIMPANZEES. *Comparative Psychology Monographs, Vol. 12, No. 5, Serial No. 60.*

By John B. Wolfe. Johns Hopkins Press, Baltimore. $1.25. 10 x 7; 72; 1936 (paper).

The experiments discussed in this paper were performed with the object of ascertaining whether tokens, in the form of poker chips, could serve as secondary or surrogate rewards for chimpanzees and if so, the relative effectiveness of such tokens in comparison with that of a primary reward, food. The results are based upon the performances of six chimpanzees in various types of tests, although not all of the animals were used in each experiment. Briefly stated, the results of this study "show that tokens came to function as secondary or surrogate rewards for chimpanzees, that in certain situations they were about as effective as food in eliciting certain kinds of behavior, and that chimpanzees can make a variety of discriminations between tokens having different reward values and can use them in harmony with their drives or motives."

INFANT BEHAVIOR. *Comparative Psychology Monographs, Vol. 12, No. 4, Serial No. 59.*

By Mandel Sherman, Irene Sherman and Charles D. Flory. Johns Hopkins Press, Baltimore. $1.50. 10 x 7; 105; 1936 (paper).

In this study new-born infants ranging in age from several hours to sixteen days were observed for behavior under relatively controlled conditions, utilizing stimuli of varied intensities. Eye responses to light stimuli were observed and also reactions due to sensitivity to pain and to pressure. The strength of hand grasp was measured and several reflexes were tested. It was found that the infant makes many directed movements in response to stimuli of an optimal sort. The results further show that "the adequacy of the pupillary reflex and the reaction to a pain stimulus increases with age, and as a corollary of these observations, the reactivity of an infant, whether reflexive or defensive, is greater the more intense the stimulus."

COMPARATIVE PSYCHOLOGY. *A Comprehensive Treatise. Vertebrates.*

By Carl J. Warden, Thomas N. Jenkins and Lucien H. Warner. The Ronald Press Co., New York. $4.50. $8\frac{3}{8}$ x $5\frac{3}{4}$; x + 560; 1936.

This volume devoted to vertebrates is the last of a three volume comprehensive treatise. It is an excellent review of the more important work which has been done in the field of experimental psychology. It should prove most useful as there is a reference for nearly every statement made and the bibliography is excellent.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

OSIRIS. *Volume I. A Volume of Studies on the History of Mathematics and the History*

of Science. Presented to Professor David Eugene Smith on his 76th Birthday (Jan. 21, 1936).

Edited by George Sarton with the cooperation of R. C. Archibald, B. M. Frick and A. Pogo. Saint Catherine Press, Bruges. 10 x 7; 777; 1936 (paper).

The indefatigable, and truly indispensable, Dr. Sarton starts off *Osiris*, his new companionate journal to the old and honored *Isis*, by devoting the initial volume to a collection of nearly 40 papers about the history of mathematics and related subjects, presented by their authors and the editor as a tribute to Professor David Eugene Smith, who has done so much for the history of science, and its flourishing Society. It is a fine gesture to a worthy recipient.

In format and typography *Osiris* is apparently to be identical with *Isis*. We hope that it may have an equally useful career.

A Philosophy of Science.

By Philip Eichler. G. P. Putnam's Sons, New York. $1.50. 8 x 5½; 111; 1936.

Do you want to know the what, why, and wherefore of motion, gravitation, neuroses, volition, atoms, cancer and all else? Why there are only two sexes, not three? This little book contains the most delightfully confused answers to these questions we have ever had the pleasure of reading. Being naturally curious about such matters, we looked up the explanation of the fair sex: the female, it appears, is "like a line of least resistance."

Texas Almanac and State Industrial Guide. *Since 1857. Texas Centennial Edition.*

The Dallas News, Dallas. 50 cents; 65 cents postpaid. 8½ x 5¾; pp. 512 + folding map; 1936 (paper).

THE PRICES OF BIOLOGICAL BOOKS IN 1936

By RAYMOND PEARL and MAUD DEWITT PEARL

Department of Biology, School of Hygiene and Public Health, Johns Hopkins University

WHEN the QUARTERLY REVIEW OF BIOLOGY began publication in 1926 the custom was inaugurated of reporting at the end of each volume on the cost of the books that had been reviewed in its columns during the year. The present paper, therefore, is the eleventh of these reports on the cost of biological books. The prices of foreign books have been converted into dollars on the basis of the exchange at the time the books were received. Table 1 shows the findings for 1936, arranged in the customary manner.

TABLE 1

Prices of Biological Books, 1936

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
Other countries	5,366	$121.33	2.26
Germany	7,501	138.01	1.84
British-American	7,711	139.20	1.81
British Government	183	2.97	1.62
France	16,503	173.98	1.05
United States	89,456	919.27	1.03
Great Britain	10,494	97.86	0.94
U. S. Government	2,036	4.25	0.21
Totals and weighted average, 1936	139,250	$1,596.87	1.147
Totals and weighted average, 1926–35 incl.	1,196,008	13,009.00	1.088

The total number of pages reviewed in 1936 is 139,250, a decrease of 2.8 per cent under 1935 but an increase of 68.6 per cent over 1926, the year in which these tabulations began. In the eleven years of the QUARTERLY REVIEW's history the books reviewed in these columns have aggregated a total of 1,335,258 pages. To American buyers these cost in the aggregate a total of $14,605.87, leading to an average price per page for the total of 1.094 cents. The weighted average cost per page of 1.147 cents for all the books reviewed in 1936 is 5.4 per cent higher than that for all the books reviewed in our columns during the preceding decade 1926–35 incl., taken as a bulk total. It is higher than the corresponding average for 1935 of 1.032 cents per page by 10.0 per cent. The 1936 average price per page for all books reviewed is 4.6 per cent higher than the corresponding figure for 1926, which was 1.097 cents.

In 1936 the "Other countries" books displaced Germany from her customary position at the head of Table 1, as the source of origin of highest prices for biological books. This is due partly to the fact that the average per page cost of our sample of German biological books fell off a little from the 1935 level, but more particularly because the "Other countries" sample for 1936 included Vosmaer's magnificent monograph on sponges, necessarily very costly to American buyers because of the unfavorable exchange at the time, and inherently so to any buyer because of the expense involved in its superb production. If this item be dropped from the "Other countries" sample, the line in Table 1 would read as follows: Total pages 4491; Total cost $36.83; Price per page 0.82 cents. Germany would then head Table 1 once more, "Other countries" would drop to seventh place, and all the other countries would

otherwise retain their same relative positions.

Table 2 shows the price trends of books published in various countries from 1927 to 1936 and the absolute and relative changes in price from 1935 to 1936 and from 1927 to 1936. In order to keep Table 2 within bounds it is necessary this year to drop off the column for 1926. In the future we shall continue to make this a table showing a decade of prices, but not more. Any reader wishing to refresh his memory regarding the more ancient history of biological book prices can do so by turning up earlier volumes of the Q. R. B.

The average prices per page of our samples of biological books from every origin except Germany were *higher* than in 1935, by amounts ranging from about 12 per cent for books commercially produced in Great Britain to well over 200 per cent for the British Government official publications. This latter percentage means little, however, because the 1936 sample was particularly small, as Table 1 shows. Biological books produced by commercial publishers in the United States in 1936 advanced in average per page price over 1935 by 14.4 per cent. On the other hand the 1936 average price per page was 5.5 per cent lower than that shown by our 1927 sample. The rise in the per page price of biological books published in France, which has been commented on in these notes in recent years, continued in 1936 and amounted to 22.1 per cent over 1935 prices and 191.7 per cent over those of a decade earlier. Furthermore the 1936 sample of French books was the largest for any single year in the history of the QUARTERLY. Our sample of biological books from British commercial publishers

TABLE 2

Comparison of the Prices of Biological Books from 1927 to 1936

ORIGIN	AVERAGE PRICE PER PAGE										CHANGE + OR − FROM 1935 TO 1936		CHANGE + OR − FROM 1927 TO 1936	
	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	Absolute	Relative	Absolute	Relative
	cents	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*per cent*	*cents*	*per cent*
British-American	1.39	1.46	1.90	1.91	2.27	1.48	1.29	1.45	1.53	1.81	+0.28	+18.3	+0.42	+30.2
Other countries	0.78	1.13*	1.68	0.97	1.53	1.02	0.85	0.86	1.20	2.26	+1.06	+88.3	+1.48	+189.7
Great Britain	1.14	1.09	1.29	1.13	1.19	0.89	0.66	0.96	0.84	0.94	+0.10	+11.9	−0.20	−17.5
United States	1.09	1.14	1.14	1.09	1.05	1.00	1.02	0.93	0.90	1.03	+0.13	+14.4	−0.06	−5.5
Germany	1.20	1.48	1.65	1.82	1.75	1.60	1.43	1.89	2.04	1.84	−0.20	−9.8	+0.64	+53.3
British Government	0.96	1.26	0.39	1.19	1.03	1.45	1.39	0.89	0.50	1.62	+1.12	+224.0	+0.66	+68.8
France	0.36	0.45	0.47	0.47	0.69	0.60	0.74	1.00	0.86	1.05	+0.19	+22.1	+0.69	+191.7
U. S. Government	0.24	0.21	0.23	0.30	0.28	0.36	0.17	0.18	0.11	0.21	+0.10	+90.9	−0.03	−12.5

* With two special treatises omitted as explained in Vol. 3, p. 601.

TABLE 3

Average Biological Book Prices over the Eleven Year Period, 1926–36 Inclusive

ORIGIN	TOTAL PAGES	AVERAGE PRICE PER PAGE
		cents
British-American	96,192	1.617
Germany	151,569	1.555
Other countries	46,173	1.364
United States	777,110	1.041
British Government	7,559	1.031
Great Britain	103,934	0.988
France	113,135	0.682
U. S. Government	39,586	0.244
Total and weighted average	1,335,258	1.094

showed an 11.9 per cent advance in price over the 1935 sample. It is interesting to note, and to emphasize, that Germany alone of all the sources of origin tabled in these reports showed a decline in average per page prices in 1936 as compared with 1935. This is presumably a reflection of the policy put into effect by Germany on Sept. 9, 1935 of granting a 25 per cent reduction in export prices on books and periodicals.

To the present report we add a new feature in Table 3, which sums up by countries of origin the whole eleven years experience of the QUARTERLY REVIEW.

A number of interesting inferences may be drawn from this table. In the first place it is evident, from what has now grown to be a substantial sample, that during the past eleven years biological books from all over the world taken together have averaged to cost the American biologist very close to a cent a page, taking good, bad, and indifferent together. Furthermore it is plain that the sources of origin of these books fall into three fairly sharply defined groups relative to unit prices to the American buyer. In the first or relatively high priced group fall books in the British-American, Germany, and "Other countries" categories of origin. The next or medium priced group includes the United States, British Government, and Great Britain (commercial publishers). The average per page cost of biological books has been very nearly the same for these origins. Finally the third or relatively low price group includes books published in France and by the U. S. Government.

The reader should bear in mind that these reports are based on small samples of books in general and, for some countries, on small samples of the biological books published. He should therefore be cautious in applying conclusions drawn from this material to the general domain of book prices.

INDEX

Abderhalden, E. (Ed.), Handbook of Biological Methods, 88, 362, 486
Abnormalities, in cyclopia, 291, 295
Adelmann, H. B., The Problem of Cyclopia, 161–182, 284–304
Agar, W. E., Whitehead's Philosophy of Organism; an Introduction for Biologists, 16–34
Albrecht, *et. al.*, Pure and Applied Sociology, 466
Alderman, A. L., Some New and Little Known Amphipods of California, 475
Aldis, R. W., A Shellac Patent Index, 474
Alexander, F., and Healy, W., Roots of Crime, 255
Allen, A. A., American Bird Biographies, 236
Amblystoma, 176, 284, 396
American Committee for Wild Life Protection, The London Convention for the Protection of African Fauna and Flora, 99
Anderson, E., and Woodson, R. E., The Species of *Tradescantia* Indigenous to the United States, 243
Androp, S., The Probability of Commitment for a Mental Disorder of any Kind Based on the Individual's Family History, 368
Arbuthnot, J., More Profit Than Gold, 467
Arkin, H., and Colton, R. R., Graphs. How to Make and Use Them, 488
Aron, M., and Grassé, P., Textbook of Zoology, 354
Auger, D., Rhythms in Action Currents, 461

Bacteria, nutritional requirements of, 406
Baitsell, G. A., Manual of Biology, 461
Baker, J. R., The Chemical Control of Conception, 226
Balfour-Browne, F., Concerning the Habits of Insects, 238
Barbour, T., and Porter, M. D., Notes on South African Wild Life Conservation Parks and Reserves, 238
Barrows, H. R., Elements of General Biology, 460
Bary, P., *et al.*, Organic Chemistry, 113
Becker, F. E., 123
Beebe, W., and Hollister, G., The Fishes of Union Island, Grenadines, British West Indies, with the Description of a New Species of Star-Gazer, 239
Bengston, N. A., and Van Royen, W., Fundamentals of Economic Geography, 231
Bennett, W. C., and Zingg, R. M., The Tarahumara, 95
Benoit, J., The Ovary, 360
The Testes, 360
Benson, S. B., A Biological Reconnaissance of Navajo Mountain, Utah, 240
Beretervide, J. J., and Rosenblatt, S., Endocrine Glands and Prostitution, 115
Bergsmark, D. R., Economic Geography of Asia, 231
Bergson, H., Thought and the Moving, 120
Bernatzik, H. A., South Seas, 349
Bertin, L., Migrations and Metamorphoses of the European Eel, 101
Besterman, T., A Bibliography of Sir James George Frazer, O.M., 350
Bews, J. W., Human Ecology, 232
Bilaterality of eyes, factors responsible for, 289
Bill, A. C., The Conquest of Death, 112
Binet, L., Scenes of Animal Life, 483
Six Lectures on Physiology, 108
et al., Lessons on Medico-Surgical Physiology, 108
Biochemical and Allied Research in India in 1934, 251
Biochemistry (book reviews), 113, 249, 362, 484
Biocoenology, 320
Biometry (book reviews), 115, 252, 365, 488
Birds, sexual cycle of, 374
Bissonnette, Thomas H., Sexual Photoperiodicity, 371–386
Blacklock, D. B., and Southwell, T., A Guide to Human Parasitology, 354
Black Rock Forest, Black Rock Forest Papers, 477
Black widow spider, 123
Boder, D. P., The Influence of Concomitant Activity and Fatigue upon Certain Forms of Reciprocal Hand Movement and Its Fundamental Components, 112
Boeuf, F., The Scientific Basis of Plant Amelioration, 458
Bohn, G., The Invertebrates, 100
Böker, H., Introduction to Comparative Anatomy of Vertebrates, 357
Bolgert, M., Diseases of the Pancreas and Functional Pancreatic Disturbances, 361
Bond, W. N., Probability and Random Errors, 365
Borradaile, L. A., and Potts, F. A., The Invertebrata, 239
Bose, *Sir* J. C. (Ed.), Transactions of the Bose Research Institute, Calcutta, 224
Botany (book reviews), 103, 240, 356, 475
Boulenger, E. G., A Natural History of the Seas, 355
Bowler, A. C., and Bloodgood, R. S., Institutional Treatment of Delinquent Boys, 464
Boyd, E., The Growth of the Surface Area in the Human Body, 252
Braarud, T., The "Ost" Expedition to the Denmark Strait, 106
Brachet, A., Embryology of the Vertebrates, 358

Breder, C. M., Jr., The Reproductive Habits of the North American Sunfishes (Family Centrarchidae), 474
and Coates, C. W., Sex Recognition in the Guppy *Lebistes reticulatus* Peters, 252
Bremer, F., *et al.*, Treatise on Normal and Pathological Physiology, 249
Brown, G. G., and Hutt, A. McD. B., Anthropology in Action, 95
Brues, Charles T., Aberrant Feeding Behavior Among Insects and Its Bearing on the Development of Specialized Food Habits, 305–319
Buffalo Society of Natural Sciences, Bulletin, 223
Bull, H. B., The Biochemistry of the Lipids, 250
Burchard, E. M. L., Physique and Psychosis, 489
Burrows, William, The Nutritional Requirements of Bacteria, 406
Buschke, F., X-Ray Studies on Human Twins, 342
Bushnell, D. I., Jr., The Manahoac Tribes in Virginia, 231
Buthine, M. A., Between the Anvil and the Hammer, 230
Buytendijk, F. J. J., The Mind of the Dog, 367

Calewaert, D., Essay on the Physical Conception of Life, 225
Carbon dioxide, 419
Carnegie Institution of Washington, Papers from Tortugas Laboratory of Carnegie Institution of Washington, 470
Carrel, A., Man the Unknown, 90
Carruthers, D., Arabian Adventure to the Great Nafud in Quest of the Oryx, 469
Castetter, E. F., Ethnobiological Studies in the American Southwest, 240
Caullery, M., French Science and Its Principal Discoveries Since the Seventeenth Century, 257
Modern Conceptions of Heredity, 224
Causation, 26
Celsus, *De Medicina*, 109
Chandler, A. C., Introduction to Human Parasitology, 354
Chapman, V. J., The Halophyte Problem in the Light of Recent Investigations, 209–220
Chassell, C. F., The Relation Between Morality and Intellect, 462
Chen, H. K., Development of the Pectoral Limb of *Necturus maculosus*, 244
Cherniss, H., Aristotle's Criticism of Presocratic Philosophy, 256
Chideckel, M., The Single, the Engaged and the Married, 365
Chinese Medical Journal, Chinese Medical Journal Supplement, 484
Chisholm, A. H., Bird Wonders of Australia, 234
Clephane, I., Towards Sex Freedom, 252
Clinton, C. A., Sex Behavior in Marriage, 252
Coefficient of dispersion, 322
Colloid Committee of the Faraday Society, Collected Scientific Papers of Sir William Bate Hardy, 342
Collum, V. C. C., The Tressé Iron-Age Megalithic Monument, 98
Compton, A. H., The Freedom of Man, 232
Cook, S. F., Elementary Human Physiology, 482
and Burmester, M. A., Laboratory Manual in Elementary Human Physiology, 482
Copson, E. T., An Introduction to the Theory of Functions of a Complex Variable, 253
Corbet, A. S., Biological Processes in Tropical Soils, 85
Cornaro, L., How to Live for a Hundred Years and Avoid Disease, 247
Cornish, V., Scenery and the Sense of Sight, 246
Costanzo, A., Constitution and Mortality, 346
Coulter, M. C., The Story of the Plant Kingdom, 242
Council on Pharmacy and Chemistry of the American Medical Association, Glandular Physiology and Therapy, 362
Cowan, I. McT., A Distributional Study of the Peromyscus Sitkensis Group of White-Footed Mice, 240
Cranial capacity, 274
Creamer, D. B., Is Industry Decentralizing? 97
Crile, G., The Phenomena of Life, 344
Crozier, W. J., Determinism and Variability in the Behavior of Organisms, 255
Cuénot, L., The Species, 222
Culver, D. C., Bibliography of Crime and Criminal Justice, 230
Cunningham, B. V., Family Behavior, 466
Curtius, F., The Organic and Functional Hereditary Diseases of the Nervous System, 248
Cutler, D. W., and Crump, L. M., Problems in Soil Microbiology, 85
Cyclopia, 161, 284
experimental production of, 167
morphology of, 162

Dallas News, Dallas, Texas Almanac and State Industrial Guide, 491
Daly, R. A., The Changing World of the Ice Age, 82
D'Amour, F. E., Becker, F. E., and Van Riper, W., The Black Widow Spider, 123–160
Dampier-Whetham, W. C. D., and Whetham, M. D., Cambridge Readings in the Literature of Science, 257
Daniel, R. J., *et al.* (Eds.), Proceedings and Transactions of the Liverpool Biological Society, 86
Dantchakoff, V., Sex Determination, 487
Daugherty, M., Sex Worship and Disease, 115

Davis, H. T., and Nelson, W. F. C., Elements of Statistics, 252
Davis, R. A., Psychology of Learning, 118
Dawson, L. H. (Eng. Ed.), The March of Man, 227
Decugis, H., The Destiny of the White Races, 91
De Omnibus Rebus et Quibusdem Aliis (book reviews), 119, 255, 369, 490
Desbarolles, A., The Hand and Its Secrets, 349
Detwiler, S. R., Neuroembryology, 477
Dhar, N. R Influence of Light on Some Biochemical Processes, 250
Dickey, F. van V., Familiar Birds of the Pacific Southwest, 102
Ditmars, R. L., Serpents of the Northeastern States, 238
and Bridges, W., Snake-Hunters' Holiday, 235
Doak, C. C., Evolution of Foliar Types, Dwarf Shoots, and Cone Scales of *Pinus*, 105
Dodd, S. C., A Controlled Experiment on Rural Hygiene in Syria, 108
Dodge, C. W., Medical Mycology, 476
Doeuvre, J., *et al.*, Organic Chemistry, 250
Dog, playing with, 1
Dollard, J., Criteria for the Life History, 345
Drew, G. A., A Laboratory Manual of Invertebrate Zoology, 474
Driesch, H., The Machine and the Organism, 84
Dublin, L. I., and Lotka, A. J., Length of Life, 229
Dubuisson, M., The Ionograms of Muscular Contraction, 112
Dufrenoy, J., Application of Statistical Methods to Plant-Pathology, 489
Duggan-Cronin, A. M., The Bantu Tribes of South America, 227
Duggar, B. M., *et al.*, Biological Effects of Radiation, 459
Dukes, H. H., The Physiology of Domestic Animals, 111

Eames, A. J., Morphology of Vascular Plants, 476
Echidna, 389
Edgeworth, F. H., The Cranial Muscles of Vertebrates, 357
Edin, K. A., and Hutchinson, E. P., Studies on Differential Fertility in Sweden, 227
Efficient causation, 26
Egypt, Board of Marine Sanitation and Quarantine of, Report on the Pilgrimage to Hedjaz, 248
Eichler, P., A Philosophy of Science, 491
von Eickstedt, E. F., Foundations of Race Psychology, 368
Elliott, C., Rock Garden Plants, 242
Ellis, H., Psychology of Sex, 364
Enduring objects, 22
End-state, 3
Ephrussi, B., Phenomena of Integration in Tissue Cultures, 87
Eternal objects, 20
Extensive continuum, 23
Evolution (book reviews), 81, 221, 341, 456

Fabre, René, Medicolegal Toxicology, 484
Fairgrieve, J., and Young, Ernest, Human Geography, 468
Feeding behavior of insects, 305
Fergusson, H., Modern Man, 233
Ferrets, sexual cycle of, 379
Fiebiger, J., Animal Parasites, 355
Fieser, L. F., The Chemistry of Natural Products Related to Phenanthrene, 362
Final causation, 26
Fisher, R. A., The Design of Experiments, 116
Fitzpatrick, F. L., and Horton, R. E., Student's Manual in Biology, 89
Flaskämper, P., and Blind, Adolph (Eds.), Contributions on German Statistics, 489
Folsom, J. W., Entomology, 102
Forest Products Laboratory, U. S. Forest Service, Wood Handbook, 242
Formosov, A. N., Fluctuations in Numbers of Game Animals, 87
Franklin Institute, Reports of the Biochemical Research Foundation, 363
Frenzel, G., Investigations of the Animal World of the Meadow-Lands, 354
Freud, Sigmund, Autobiography, 234
Frommolt, G., Race Problems in Obstetrics and Gynecology, 233
Frontal sinuses, 269,
Fry, C. C., and Haggard, H. W., The Anatomy of Personality, 468
Fulton, J. F., A Bibliography of Two Oxford Physiologists, Richard Lower and John Mayow, 361
Fundulus, 167
Furnas, C. C., The Next Hundred Years, 257

Ganglia, 392
Gangulee, N., The Indian Peasant and His Environment, 92
Gause, G. F., The Principles of Biocoenology, 320–336
Experimental Proofs of the Mathematical Theory of the Struggle for Existence, 222
Gebbing, J., A Life for Animals, 353
Geipel, G., Introduction to the Genetic Examination of Finger and Hand Prints, 83
Gene, 57
General Biology (book reviews), 84, 224, 342, 459
Genetics (book reviews), 82, 223, 342, 458
Given, D. H. C., A New Angle on Health, 110

Glassell, S. A., New or Little Known Crabs from the Pacific Coast of Northern Mexico, 103
Good, N. E., The Flour Beetles of the Genus Tribolium, 470
Goodrich, C., *et al.*, Migration and Planes of Living, 94
Gorer, G., Africa Dances, 231
Goulden, C. H., Methods of Statistical Analysis, 489
Grabau, A. W., Studies of Gastropoda, 235
Graham, S. A., The Spruce Budworm on Michigan Pine, 102
Greaves, J. E., and Greaves, E. O., Elementary Bacteriology, 356
Greene, E. C., Anatomy of the Rat, 244
Greenwood, Major, The Medical Dictator and Other Biographical Studies, 465
Gregory, J., A B C of the Endocrines, 249
Grignard, V., and Baud, P., Textbook of Organic Chemistry, 486
Grinnell, J., Differentiation in Pocket Gophers of the Thomomys Bottae Group in Northern California and Southern Oregon, 240
Grollman, A., The Adrenals, 480
Grove, W. B., British Stem- and Leaf-Fungi, 105
Growth, of man and the great apes, 267
stimulating substances, 416
Günther, H., Variability of Organisms and Their Normal Limits, 366
Guyénot, É., The Determination of Sex and Heredity, 363
Guyer, M. F., Animal Micrology, 478

Habitat, black widow spider, 125
Haglund, S., Life Among the Lapps, 228
Hale, A. R., The Medical Voodoo, 248
Hall, E. R., Nevadan Races of the Microtus Montanus Group of Meadow Mice, 240
Hall, G. M., Prostitution in the Modern World, 365
Halliday, W. M., Potlatch and Totem, 230
Halophyte problem, 209
Halstead, W., The Effect of Cerebellar Lesions upon the Habituation of Post-Rotational Mystagmus, 246
Hambly, W. D., Culture Areas of Nigeria, 96
Hand, proportions of, 434
Harris, L. J., Vitamins in Theory and Practice, 250
Hart, A. B., and Cox, I. J., (Am. Eds.), The March of Man, 227
Hartman, C. G., Time of Ovulation in Women, 365
Hartman, O., New Species of Spinoidae (Annelida Polychaeta), 475
Hatt, P., Morphogenetic Processes in the Development of the Vertebrates, 479
Hayner, J. C., Regional Anatomy, 243
Head, proportions of, 441
Health and Efficiency Holiday Annual, 113
Health Organisation, League of Nations, Quarterly Bulletin, 113, 249
Hegner, R. W., College Zoology, 472
Parade of the Animal Kingdom, 99
Hering, M., The Leaf Burrows of Central and Northern Europe, 239, 474
Herrick, G. W., Insect Enemies of Shade-Trees, 236
Hesse, R., Evolution and Darwinism, 457
Higgins, V., and Marrable, H. T., Cactus Growing for Beginners, 105
Higher primates and man, 425
Himes, N. E., Medical History of Contraception, 486
Hirschfeld, M., Sex in Human Relationships, 251
Hitschmann, E., and Bergler, E., Frigidity in Women, 488
Holden, W. C., *et al.*, Studies of the Yaqui Indians of Sonora, Mexico, 348
Holmes, M. E., An Outline of Probability and Its Uses, 366
Hort, *Sir* A. F., Garden Variety, 242
Howell, A. Brazier, Morphogenesis of the Shoulder Architecture, Part IV, Reptilia, 183–208
Howell, A. Brazier, 387
Hrdlička, A., Melanesians and Australians and the Peopling of America, 232
Hubbell, T. H., A Monographic Revision of the Genus Ceuthophilus, 470
Huey, E. G., A Child's Story of the Animal World, 355
Huey, L. M., A New Silky Pocket Mouse from Sonora, Mexico, 103
Human Biology (book reviews), 89, 227, 345, 462
Huntington, E., *et al.*, Tomorrow's Children, 350
Hurley, V., Men in Sun Helmets, 350
Hurst, C. C., Heredity and the Ascent of Man, 81
Huxley, E., White Man's Country, 94
Huxley, J. (Ed.), T. H. Huxley's Diary of the Voyage of H. M. S. Rattlesnake, 459
Huxley, J. S., Problems in Experimental Embryology, 87
Hyatt, H. M., Folk-Lore from Adams County, Illinois, 98
Hylobatidae, 270, 433

Iguana, morphogenesis of shoulder architecture, 186
Immunology, 149
Initial data, 19
Insects, aberrant feeding behavior of, 305
Institute of Actuaries and Faculty of Actuaries in Scotland, Continuous Investigation into the Mortality of Assured Lives, 253
International Federation of Eugenic Organizations, Report of the 11th Assembly, 83
International Labor Office, Geneva, Occupation and Health, 482

Iovetz-Tereshchenko, N. M., Friendship-Love in Adolescence, 487
Ischial callosities in the great apes, 265
Israeli, N., Outlook upon the Future of British Unemployed, Mental Patients, and Others, 97
Ivanoff, N. N. (Ed.), Biochemistry of Cultivated Plants, 357
Ives, J. E., *et al.*, Atmospheric Pollution of American Cities, 461

Jaffe, B., Outposts of Science, 255
Jankowsky, W., Blood Relationship, 83
Järvi, T. H., and Menzies, W. J. M., The Interpretation of the Zones on Scales of Salmon, Sea Trout and Brown Trout, 472
Jarvis, C. S., *et al.*, Floods in the United States, 461
Jennings, H. S., Genetics, 82
Genetic Variations in Relation to Evolution, 223
Johnson, M. E., and Snook, H. J., Seashore Animals of the Pacific Coast, 473
Jordan, D. S., A Classification of Fishes, 103
Jordan, E. O., A Textbook of General Bacteriology, 106
Jürgens, G., Foundations of Epidemiology, 482

Kanner, L., Child Psychiatry, 119
Katzenelbogen, S., The Cerebrospinal Fluid and Its Relation to the Blood, 247
Keep, J., West Coast Shells, 101
Kelley, T. L., Essential Traits of Mental Life, 367
and Krey, A. C., Tests and Measurements in the Social Sciences, 96
Kelway, Phyllis, Hedge Folk in Twilight, 474
Kemp, P., Healing Ritual, 234
Kempermann, C. T., Turning Point in Phylogeny, 342
Kendall, W. C., The Fishes of New England, 236
Kenly, J. C., Cities of Wax, 239
Kirk, S. A., Hemispheric Cerebral Dominance and Hemispheric Equipotentiality, 248
Klauber, L. M., A New Subspecies of *Crotalus confluentus*, the Prairie Rattlesnake, 103
Crotalus Mitchellii, the Speckled Rattlesnake, 475
Klein, W., (Ed.), The Hereditarily Sound and the Hereditarily Diseased, 347
Klem, Alf, Chemical Analysis of the Samples of Blue Whale Oils, 249
Kluger, J. (Ed.), Researches on Longevity, 86, 484
Knapp-Fisher, H. C., The World of Nature, 89
Kofoid, C. A., *et al.*, The Cycle of Trypanosoma Cruzi in Tissue Culture of Embryonic Heart Muscle, 240
Koltzoff, N. K., Physiology of Development and Genetics, 84
Komarov, V. L., The Origin of Plants, 342
Kostitzin, V. A., Evolution of the Atmosphere, 221
Krafka, J., A Textbook of Histology, 477
Krieger, L. C. C., The Mushroom Handbook, 475
de Kruif, Paul, and de Kruif, Rhea, Why Keep Them Alive? 369
Kuczynski, R. R., The Measurement of Population Growth, 349
Külbs, F., Healthy Life, 112

Lacape, R. S., Physiological Time, 483
Lakhovsky, G., Cellular Oscillation, 109
Matter, 119
The Secret of Life, 109
Lamond, H. G., An Aviary on the Plains, 354
Landsteiner, K., The Specificity of Serological Reactions, 358
Langdon-Brown, *Sir* Walter, The Integration of the Endocrine System, 359
Lartschneider, J., Cancer, 113
Lasorsa, G., The Legitimate Fertility of Women by Age, 115
Latrodectus, 127
Layman, J. D., The Avian Visual System, 361
League of Nations, Report of the Pan-African Health Conference held at Johannesburg, November 20th to 30th, 1935, 484
Leakey, L. S. B., Kenya, 464
Lee, R. E., Man the Universe-Builder, 256
Lehmann, F. M., Logic and System of the Sciences of Life, 89
Lelu, P., The Chemical Relationship of Animals, 486
Lepidoptera, 307
Lester, P., and Millot, J., The Human Races, 466
Lévy-Bruhl, L., Primitives and the Supernatural, 93
Lewin, K., A Dynamic Theory of Personality, 118
Libby, M. S., The Attitude of Voltaire to Magic and the Sciences, 256
Liesegang, R. E., Colloid Chemistry for Physicians, 363
Life, Whitehead's conception of, 31
Limb, proportions of, 432
Lincoln, F. C., The Migration of North American Birds, 353
Lösch, A., Considerations on the Decline in the Birth Rate, 233
de Loureiro, J. A., Intoxication, 361
Lovejoy, A. O., and Boas, G., A Documentary History of Primitivism and Related Ideas, 89
Luck, J. M. (Ed.), Annual Review of Biochemistry, 485
Lumby, J. R., Salinity and Temperature of the English Channel, 344
Salinity and Temperature of the English Channel. Atlas of Charts, 344
Lumière, A., Rebirth of Humoral Medicine, 360
Lyell, D. D. (Ed.), African Adventures, 351

Lynn, E., The Red Spears of Honan, 234
Lyon, M. W., Jr., Mammals of Indiana, 352

MacGinitie, G. E., Ecological Aspects of a California Estuary, 226
Macmillan, W. M., Warning from the West Indies, 467
Madison, H. L., Florida Fishes, 356
Turtle Shields, 355
Maeterlinck, M., Pigeons and Spiders, 472
Maier, N. R. F., and Schneirla, T. C., *Principles of Animal Psychology*, 254
Major, R. H., Disease and Destiny, 359
Malinowski, Bronislaw, Coral Gardens and Their Magic, 462
Mallet, R., Dementia, 119
Maltz, M., New Faces—New Futures, 481
Man, characters specific for, 259
Mantegazza, P., Physiology of Love, 364
The Sexual Relations of Mankind, 114
Marett, J. R. de la H., Race, Sex, and Environment, 221
Marett, R. R., Head, Heart and Hands in Human Evolution, 81
Marie-Victorin, Frère, Some New Statistical Results Concerning the Vascular Plants of Quebec, 476
Marshall, C., An Introduction to Human Anatomy, 243
Marshall, Clyde, The Functions of the Pyramidal Tracts, 35–56
Maximum salinities, 215
McComas, H. C., Ghosts I Have Talked With, 253
McCrady, E., Reason and Revelation, 456
McDougal, W., Religion and the Science of Life, 225
McGraw, M. B., Growth: A Study of Johnny and Jimmy, 117
McKeown, K. C., Insect Wonders of Australia, 234
McKinley, E. B., A Geography of Disease, 245
Mellen, I. M., and Lanier, R. J., 1001 Questions Answered about Your Aquarium, 237
Mengarelli, C., Constitution in Italian Aristocracies, 96
Meyer, A. W., An Analysis of the *De Generatione Animalium* of William Harvey, 471
Meyer, B. S., and Anderson, D. B., Laboratory Plant Physiology, 241
Mickel, C. E., Mutillidae of the Philippine Islands, 240
The Mutillid Wasps of the Islands of the Pacific Ocean, 240
Microbiology, Studies from the Laboratories of Microbiology, Nancy, 227
Minimum area, 324
Minz, B., Secretion of Adrenalin, Its Neuro-Humoral Mechanism, 483
Mittasch, A., On the Catalytic Factors in Biological Phenomena, 363
Molisch, H., Memories and World Impressions of a Natural Scientist, 233
de Monfried, H., Hashish, 98
Monteil, G., The Egg, 459
Morphological conception of gene, 58
Morphology (book reviews), 107, 243, 357, 477
Morton, D. J., The Human Foot, 244
Motor-nuclei, 388
Muenscher, W. C., Weeds, 103
Müller-Freienfels, R., The Evolution of Modern Psychology, 118
Muller, H. J., Out of the Night, 348
Murphy, R. C., Oceanic Birds of South America, 351
Muscles, of shoulder, 194

Needham, J., Order and Life, 343
Neonate activities, 70
Nerve-muscle action, 205
Nerves, of shoulder, 191
Nesbitt, L. M., Desolate Marches, 350
Neural plate, 285
New Biological Books, 81–121, 221–257, 337–370, 456–491
Newman, Horatio H., Outlines of General Zoology, 474
Newton, W. H. (Ed.), Evans' Recent Advances in Physiology, 481
Nexus, 29
Norberg, I., Good Food from Sweden, 97
Novak, E., The Woman Asks the Doctor, 112
Nutritional requirements of bacteria, 406

Objective datum, 19
Odell, C. W., Statistical Method in Education, 117
Ogden, E. C., The Herbaceous Flowering Plants, 106
Okkels, H., The Parathyroids, 483
Optic anlagen, 175
Organism, Whitehead's philosophy of, 16
Organization, principles of, 327
problem of, 64

Palazzoli, M., Male Sexual Impotence, 115
Paramecium, 330
Parasitic habits, change to phytophagous, 313
Pariser, K., Numerical Sex Ratio in Hybrids Obtained by Artificial Fecundation in *Triton*, 458
Parker, E., Ethics of Egg-Collecting, 236
Patch, E. M., and Howe, H. E., The Work of Scientists, 121
Patten, C. A., *et al.*, Sensation: Its Mechanisms and Disturbances, 247
Paulian, R., Polymorphism in the Males of the Coleoptera, 101

Payne, F., and Spieth, E. W., An Open Letter to College Teachers, 256
Peacock, H. A., Elementary Microtechnique, 107
Pearl, Raymond, and Pearl, Maud DeWitt, Prices of Biological Books, 492
Pearse, A. S., The Migrations of Animals from Sea to Land, 353
Pearson, S. V., The Growth and Distribution of Population, 98
Pelvis, 425
Pennell, V., A Handbook of Urology for Students and Practitioners, 483
Penniman, T. K., A Hundred Years of Anthropology, 345
Perceptual worlds, 6
Perry, W. J., The Primordial Ocean, 228
Peters, C. C., and Van Voorhis, W. R., Statistical Procedures and Their Mathematical Bases, 117
Peters, J. P., Body Water, 480
Petersen, W. F., The Patient and the Weather, Vol. 1, Pt. 1, The Footprints of Asclepius, 245
and Milliken, M. E., The Patient and the Weather, Vol. 1, Pt. 2, Autonomic Integration, 479
Pettingill, O. S., Jr., The American Woodcock *Philohela minor* (Gmelin), 472
Pettit, A., Antipoliomyelitis Serum Therapy of Animal Origin, 481
Phillips, M. E., and Cox, L. E., The Teaching of Biology, 86
Photoperiodicity, 373
Physiological conception of gene, 60
Physiology and Pathology (book reviews), 108, 245, 358, 479
Phytophagous habits, change to saprophagous, 312
Pickard, E. A., Frogs, Toads, and Salamanders, 102
Pittard, Eugène, Castration of Man and the Morphological Modifications Which Follow, 251
Playing with a dog, 1
Pleydell-Bouverie, C., Objective Evolution, 457
Policard, A., Six Lectures on Normal and Pathological Histophysiology, 478
Pratt, H. S., A Manual of Land and Fresh Water Vertebrate Animals of the United States, 102
Pratt, Karl C., Problems in the Classification of Neonate Activities, 70–80
Predatory habits of insects, 307
habits, change to phytophagous, 310
Prehension, 19
Prenant, M., Textbook of Zoology, 473
Presiding occasions, 33
Price, H., A Report on Two Experimental Fire-Walks, 367
Prices of Biological Books, 492
Primates, higher, 260
Principles of biocoenology, 320
Problem of cyclopia, 161, 284
Protozoa, experimental biocoenosis of, 331
Pryor, H. B., Width-Weight Tables, 366
Psychology and Behavior (book reviews), 117, 253, 366, 489
Puxley, W. L., Deep Seas and Lonely Shores, 461
Pyramidal tracts, functions of, 35

Rahn, O., Invisible Radiations of Organisms, 343
Ranson, S. W., The Anatomy of the Nervous System, 108
Rayment, T., A Cluster of Bees, 337
Reproduction, of black widow spiders, 127
Rice, E. L., An Introduction to Biology, 88
Rice, T. B., A Textbook of Bacteriology, 104
Richards, A., and Ortenburger, A. L., Practical Comparative Embryology, 244
Ripps, I. (Ed.), The Journal of Biological Education, 226
Rittershaus, Ernst, Constitution or Race? 229
de Rivas, D., and de Rivas, C. T., Clinical Parasitology and Tropical Medicine, 112
Roberts, E. A., and Lawrence, J. R., American Ferns, 107
Roberts, L. J., Nutrition Work With Children, 111
Roberts, S. H., The Squatting Age in Australia 1835–1847, 463
Robinson, V. (Ed.), Encyclopaedia-Dictionary of the Sexual Sciences, 364
Robinson, W. A., Voyage to Galapagos, 348
Robson, G. C., and Richards, O. W., The Variation of Animals in Nature, 456
Robson, W. A., Civilization and the Growth of Law, 92
Roche, J., Monograph on the General and Comparative Biochemistry of the Respiratory Pigments, 486
Roehl, K. McC., and Newman, H. H., A Laboratory Manual for General Zoology, 474
Romer, A. S., and Grove, B. H., Environment of the Early Vertebrates, 223
Rosendahl, C. O., *et al.*, J. Arthur Harris, 475
van Rossem, A. J., A New Race of Brown Towhee from the Inyo Region of California, 103
Notes on Birds in Relation to the Faunal Areas of South-Central Arizona, 475
The Mangrove Warbler of North-Western Mexico, 103
Ross, R. C., A New Genus and Species of Pigmy Goose from the McKittrick Pleistocene, 103
Ross, T. A., An Enquiry into Prognosis in the Neuroses, 366
Russell, E. S., Playing with a Dog, 1–15

Sabrazès, J., and Saric, R., Mononucleoses, Agranulocytoses, Aleukemic Leukemias, 111

Salinity, of soil, 209
Sarton, George (Ed.), Osiris, 490
Savory, T. H., The Arachnida, 99
Scanga, G. (Ed.), Bulletin of Vocational Guidance, 468
Schebesta, P., and Lebzelter, V., Anthropology of the Central African Pygmies in the Belgian Congo, 348
Schenk, E. T., and McMasters, J. H., Procedure in Taxonomy, 351
Schmalhausen, J., *et al.*, (Eds.), Growth of Animals, 88
Schmidt, H., Introduction to Palaeontology, 222
Schmidt, P. J., Anabiosis, 84
Schoenichen, W., Primeval Germany, 89, 226, 345
Schoorl, P., Sodium Deficiency in Rats, 114
Schrieke, B., Alien Americans, 467
Schultz, A. H., Characters Common to Higher Primates and Characters Specific for Man, 259–283, 425–455
Schultz, Br. K., and Hesch, M., Determination Charts for Eye, Hair and Skin Color, 350
Schulz, B., Genetics in Medicine, 458
Schulze, K., Homeopathic Medicines, 362
Scott, G. G., and Kendall, J. I., The Microscopic Anatomy of Vertebrates, 107
Sears, P. B., Deserts on the March, 226
Seifriz, W., Protoplasm, 345
Sensory nuclei, 391
Sex (book reviews), 114, 251, 363, 486
Sexual photoperiodicity, 371
Shapiro, H. L., The Heritage of the Bounty, 463
Shattuck, G. C. (Ed.), Handbook of Travel, 120
Sherman, M., *et al.*, Infant Behavior, 490
Shiras, G., 3d., Hunting Wild Life with Camera and Flashlight, 353
Shoulder architecture, morphogenesis of, 183
Shull, A. F., Evolution, 341
Shumway, W., Introduction to Vertebrate Embryology, 108
Silva Fennica, 357
Singer, E., Fasciae of the Human Body and Their Relations to the Organs They Envelop, 243
Skeleton, of shoulder, 183
Slemons, J. M., John Whitridge Williams, 232
Smillie, W. G., Public Health Administration in the United States, 111
Smith, K. M., Plant Viruses, 106
Snodgrass, R. E., Principles of Insect Morphology, 107
Snyder, T. E., Our Enemy the Termite, 352
Societies, 30
Spaulding, E. G., A World of Chance, 369
Speck, F. G., Naskapi, 94
Speransky, A. D., A Basis for the Theory of Medicine, 359
Spider, black widow, 123
Spinal accessory nerve and its musculature, 387
  column, of primates, 278
Stabilization, 329
Stafford, G. T., *et al.*, Individual Exercises, 113
Straus, William L., and Howell, A. Brazier, The Spinal Accessory Nerve and Its Musculature, 387–405
Ströer, W. F. H., The Gene, Its Function and Its Meaning in Genetics, 57–69
Subjective aim, 19
  form, 25
Sumner, W. G., Essays of, 93
Sutherland, H., Laws of Life, 349
Sutton, G. M., The Juvenal Plumage and Postjuvenal Molt in Several Species of Michigan Sparrows, 102
Swiss Society of Anthropology and Ethnology, 350
Széchenyi, Count Z., Land of Elephants, 351

Tauber, H., Experimental Enzyme Chemistry, 486
Taussig, F. J., Abortion, 346
Taylor, C. C., Agriculture in Southern Africa, 97
Taylor, W. P., Ecology and Life History of the Porcupine (*Erethizon Epixanthum*), 238
Tchernavin, T., We Soviet Women, 229
Tee-Van, J., *et al.*, Scientific Contributions of the New York Zoological Society, 240
Thomas, M., Plant Physiology, 241
Thomas, P., Manual of Biochemistry, 485
Thoms, H., Classical Contributions to Obstetrics and Gynecology, 249
  The Obstetric Pelvis, 244
Thomson, D. F., Birds of Cape York Peninsula, 473
Thorndike, E. L., *et al.*, Adult Interests, 117
Tian, A., and Roche, J., Textbook of Chemistry, 363
Tilden, J. E., The Algae and Their Life Relations, 104
Timirjaseff-Institute for Biology, Moscow, Problems of Theoretical Biology, 344
Timmermans, J., Binary Solutions of Organic Compounds, 485
Todd, J. C., and Sanford, A. H., Clinical Diagnosis by Laboratory Methods, 113
Toxicity, 137
Toxicology, 153
Treadwell, A. L., Polychaetous Annelids from the Vicinity of Nonsuch Island, Bermuda, 474
Treloar, A. E., An Outline of Biometric Analysis, 488
Triton, 179, 289
Tsang, Yü-Chüan, The Functions of the Visual Areas of the Cerebral Cortex of the Rat in the Learning and Retention of the Maze, 255
Tveraaen, I., Contributions to the Study of Whale Oils, 249

Ungerer, E., Periodic Phenomena in Biology, 460

University of Colorado Studies, 121
Uvarov, B. P. (Ed.), The Locust Outbreak in Africa and Western Asia in 1934, 235
van Uven, M. J., Mathematical Treatment of the Results of Agricultural and Other Experiments, 253

Valence, 3, 9
Van Riper, W., 123
Vavilov, N. I. (Ed.), Theoretical Basis of Plant Breeding, 82
Verdoorn, Fr. (Ed.), *Chronica Botanica*, 104
Verhulpen, E., Baluba and the Balubais of Katanga, 465
Vertebrae, coccygeal, 273
Visscher, M. B., and Smith, P. W., Experimental Physiology, 110
Volterra, V., and d'Ancona, U., Biological Associations from the Mathematical Point of View, 88
Vosmaer, G. C. J., The Sponges of the Bay of Naples, Porifera Incalcaria, 469

Waddington, C. H., How Animals Develop, 478
Wade, J. S., A Contribution to a Bibliography of the Described Immature Stages of North American Coleoptera, 237
Waksman, S. A., Humus, 356
Walton, E. P., and Foss, P. E., Social Biology, 460
Wardel, R. A., General Entomology, 471
Warden, C. J., The Emergence of Human Culture, 457
et al., Comparative Psychology, 254, 490
Watkins, A. E., Heredity and Evolution, 342
Weber, E., Introduction to the Statistics of Variation and Genetics, 253
Wechsler, D., The Range of Human Capacities, 115
Wegner, R. N., Indian Races and Vanished Cultures, 96
Weisenburg, T., *et al.*, Adult Intelligence, 368
Weling, A. N., The Katkaris, 98
Wellhouse, W. H., and Hendrickson, G. O., College Biology, 461
Westaway, F. W., The Endless Quest, 120
Whedon, W. F., Spawning Habits of the Mussel *Mytilus Californianus* Conrad, 475
and Kofoid, C. A., Dinoflagellata of the San Francisco Region, 475
Wheeler, W. M., A Notable Contribution to Entomology, 337–341
Whetham, M. D., 257
White, C. L., and Renner, G. T., Geography. An Introduction to Human Ecology, 465
White, F. W., Birth Control and Its Opponents, 114
Whitehead's philosophy of organism, 16
Whitfield, F. G. S., and Wood, A. H., An Introduction to Comparative Zoology, 100
Whitnall, S. E., The Study of Anatomy, 479
Whitney, L., Primitivism and the Idea of Progress, 233
Williams, J. F., Atlas of Human Anatomy, 478
Williams, J. J., *S. J.*, Africa's God, I—Gold Coast and Hinterland, 468
Willmer, E. N., Tissue Culture, 87
Willoughby, C. C., Antiquities of the New England Indians, 228
Wishart, J., and Sanders, H. G., Principles and Practice of Field Experimentation, 241
Wodehouse, R. P., Pollen Grains, 240
Wolf, A., A History of Science, Technology, and Philosophy in the 16th and 17th Centuries, 119
Wolf, B., Catalogue of Cavern Fauna, 103
Wolfe, J. B., Effectiveness of Token-Rewards for Chimpanzees, 490
Woodruff, L. L., Foundations of Biology, 460
Wright, F. S., Report on the Maldon (Essex) Periwinkle Fishery, 355
Conditions of Certain of the Oyster Beds in the South Wales Sea Fisheries District, 355
Wright, G. M., and Thompson, B. H., Fauna of the National Parks of the United States, 100
Wrist bones, 271
Wurmser, R., Electroactivity in Cellular Chemistry, 114

Zilboorg, G., The Medical Man and the Witch during the Renaissance, 91
Zirkle, C., The Beginnings of Plant Hybridization, 223
Zoethout, W. D., A Textbook of Physiology, 247
Zondek, H., The Diseases of the Endocrine Glands, 110
Zoology (book reviews), 99, 234, 351, 469